
JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 52

JANUARY 1971

NUMBER 1

EMBRYOLOGY OF THE MAGNOLIALES AND COMMENTS
ON THEIR RELATIONSHIPS¹

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EVER SINCE THE PROPOSAL of Bennettitalian origin of angiosperms, the magnolian complex and particularly the Magnoliaceae, have occupied a pivotal position in all phylogenetic considerations, since in the "Magnolia flower" the proponents of this theory visualized all the representative analogous reproductive parts in the Bennettitalian fructification.

No doubt the various theories to interpret the angiosperm flower and its appendages, such as the telome theory (*see* Zimmermann, 1955; Wilson, 1937, 1942, 1953; Wilson & Just, 1939), gonophyll theory (Melville, 1962, 1963) and interpretation of the angiosperm flower (Barnard, 1961; Sporne, 1949) are exhaustive mental exercises based directly on the extinct plants. However, the fast emerging fact is that the living ranalian members should be subjected to an extensive survey from all points of view, in order to understand, if not the origin of the angiosperms, at least the basic primitive patterns and their further diversifications during the course of phylogeny. Consequently, this resulted in a concerted effort to investigate fully the morphology, anatomy, and embryology of this interesting group of the dicotyledons.

It is rather fortunate that the group attracted the attention of two doyens of plant morphology and embryology, Professor I. W. Bailey and Professor P. Maheshwari, who established strong schools in their respective fields to gain an insight into the ranalian complex. By coordinated effort over a span of 30 years or more Professor I. W. Bailey and his colleagues have projected explicitly the basic primitive morphological and anatomical patterns and their amplification, in ascending or descending phylogenetic series, in numerous ranalian families. Their efforts have resulted in studies on the Magnoliaceae (Canright, 1952a,b; 1955; 1960; 1965), Degeneriaceae (Bailey & Smith, 1942; Swamy, 1949), Winteraceae (Bailey, 1944b; Bailey & Nast, 1943a,b; 1944a,b; 1945; Nast, 1944), Himantandraceae (Bailey, Nast, & Smith, 1943), Schisandraceae

¹ Dedicated to the memory of the late Professor P. Maheshwari, a renowned embryologist and my teacher, and the late Professor I. W. Bailey, a great plant anatomist and morphologist.

and Illiciaceae (Bailey & Nast, 1948; Smith, 1947), Austrobaileyaceae (Bailey & Swamy, 1949), Trimeniaceae and Monimiaceae (Money, Bailey, & Swamy, 1950), Amborellaceae (Bailey, 1947; Bailey & Swamy, 1948), Gomortegaceae (Money, Bailey, & Swamy, 1950), Trochodendra-ceae and Tetracentraceae (Bailey & Thompson, 1918; Bailey & Nast, 1945; Nast & Bailey, 1945; Smith, 1945), Eupteleaceae (Nast & Bailey, 1946; Smith, 1946), and Cercidiphyllaceae (Bailey & Nast, 1945; Nast & Bailey, 1945; Swamy & Bailey, 1949).

On the other hand, Professor P. Maheshwari interested some of his pupils in taking up a study of the embryology of some ranalian families. They have contributed substantially towards our knowledge of such families as the Magnoliaceae (Bhandari, 1967a; Kapil & Bhandari, 1964), Degeneriaceae (Bhandari, 1967b), Himantandraceae (Vijayaraghavan & Bhandari, 1970), Winteraceae (Bhandari, 1963b, 1967c; Bhandari & Venkataraman, 1968), Myristicaceae (Bhandari, 1967d), Canellaceae (Bhandari, 1967e), Schisandraceae (Bhandari, 1967f; Jalan & Bhandari, 1963; Jalan & Kapil, 1965; Kapil & Jalan, 1964), Illiciaceae (Bhandari, 1967g), Monimiaceae (Bhandari, 1967h), Calycanthaceae (Bhandari, 1967i), Lauraceae (Bhandari, 1967j), Trochodendraceae (Bhandari, 1967k), Cercidiphyllaceae (Bhandari, 1967l), Chloranthaceae (Vijayaraghavan, 1964), and Ranunculaceae (Bhandari, 1962, 1963a, 1965, 1966, 1968; Bhandari & Asnani, 1968; Bhandari & Kapil, 1964; Bhandari & Vijayaraghavan, 1970; Jalan, 1963; Jalan & Bhandari, 1963; Kapil & Jalan, 1962; Vijayaraghavan, 1962, 1963; Vijayaraghavan & Bhandari, 1970; Vijayaraghavan & Marwaha, 1969a,b).

Erdtman (1952), Erdtman & Metcalfe (1963), and Wodehouse (1935, 1936) have contributed immensely towards the study of pollen morphology and its application in systematics. Pollen characters no doubt form one of the fundamental features in considering interrelationships amongst various families and must be fully utilized.

The chromosome number and the karyotypic studies can be very meaningful in considering interrelationship within this interesting group. Unfortunately, as compared to the large number of taxa included in this order, chromosome numbers for only a few of them have been worked out. Furthermore, as pointed out by Raven and Kyhos (1965), the chromosome counts for not even a single species of one of the primitive families, the Winteraceae, as summarized by Darlington and Wylie (1955) stands correct today. This fact stresses the need for rechecking of the basic number reported during the 1930's. As pointed out earlier, karyotype might have an important bearing on the interrelationship amongst the various primitive families. Such precise studies are wanting; however, recent investigations by Rüdénberg (1967), Stone (1968), and Stone and Freeman (1968) are welcome additions.

It is fully realized that although it is not possible to erect a phylogenetic system of classification based on embryological characters alone, it is also not tenable with any other single series of characters. However, that the embryological characters play an important role in deciding the inter-

relationships in particular instances has been amply emphasized by Maheshwari (1950a,b, 1954, 1956, 1959, 1963, 1964), Johri (1963), Kapil (1962), Subramanyam (1962), and Cave (1959). Therefore, an attempt like the present one to tabulate and evaluate the embryological evidences in conjunction with others in phylogenetic considerations of the Magnoliales needs no justification.

The order Ranales *sensu lato* has undergone tremendous changes because of the injunction of phylogeny in taxonomy (Cronquist, 1968; Engler, 1964; Takhtajan, 1966; Thorne, 1968) and there have been many additions or deletions from one family to another and *vice versa*. Furthermore, a large number of taxa have been excluded from or included in this group by one or the other taxonomist. In this review I have followed the recently proposed system by Cronquist (1968) which includes 19 families in the order Magnoliales, comprising chiefly the woody members of the ranalian complex.

The families Trochodendraceae and Cercidiphyllaceae have also been included although these along with Tetracentraceae and Eupteleaceae are placed in the orders Trochodendrales and Hamamelidales. This system (Cronquist, 1968) has been followed only to have a framework for the review without giving due consideration to any of its phylogenetic implications. Embryological information on Lactoridaceae, Eupomatiaceae, Trimeniaceae, Amborellaceae, Gomortegaceae, Hernandiaceae, Tetracentraceae and Eupteleaceae is wanting. These have, therefore, been excluded from the description of the families, but since well established relationships have been shown based chiefly on the morphological and anatomical evidence I have included some of these families in the discussion on interrelationships of the Magnoliales in order to make the evaluation as complete as possible.

EMBRYOLOGY AND CYTOLOGY

Austrobaileyaceae. The family comprises a single genus, *Austrobaileya*, with two species distributed in Australia. Embryological information is meager and according to Davis (1966) is unknown; perhaps she overlooked the passing reference made by Bailey and Swamy (1949) concerning some points in the anther wall development and male gametophyte. The wall of the young microsporangium comprises the epidermis, three wall layers, and an irregularly two-layered glandular tapetum having binucleate cells. At maturity the epidermal cells become protuberant, the endothelial cells enlarge but it could not be made out from the illustrations whether these develop characteristic fibrous bands or not. The middle layers and the tapetum become absorbed and only their remnants are perceptible. Cytokinesis is simultaneous. As in *Degeneria* the exine formation begins while the microspores are still in tetrads. The germinal furrow develops along the distal face where also the generative cell is cut off. The mature pollen is spherical, monocolpate with colpus extending from one pole to the other; the exine is finely pitted. The external

surface of the furrow possesses minute protuberances. Rüdénberg (1967) has investigated the karyotype of *Austrobaileya* and found $2n = 44$. The basic number in the family would be $x = 22$.

Magnoliaceae. The Magnoliaceae are distributed primarily in eastern Asia, Malesia, southeastern North America, Central America, the West Indies, and Brazil. In India the family is represented by 22 species belonging to 5 genera. Embryological literature concerns only *Magnolia* (Brandza, 1891; Earle, 1938a,b; Farr, 1918; Hayashi, 1960, 1964; Kapil & Bhandari, 1964), *Michelia* (Padmanabhan, 1960) and *Liriodendron* (Kaeiser & Boyce, 1962).

The anther wall at the microspore mother cell stage comprises the epidermis, endothecium, 3 or 4 middle layers and bilayered glandular tapetum (FIGURE 1 A). By the time the cytokinesis is completed in the microspore mother cells, a large number of Ubisch granules line the inner walls of the tapetum. In a fully mature anther the papillate epidermis and endothecium along with 2 or 3 middle layers persist (FIGURE 1 B). In *Magnolia stellata* (Kapil & Bhandari, 1964) the endothecium possesses reticulate thickenings instead of the usual fibrous bands found in other members. After meiosis II in the microspore mother cells the cytokinesis takes place by furrowing (FIGURES 1 C, D), resulting in tetrahedral or isobilateral tetrads (FIGURE 1 E). The mature pollen is monocolpate (FIGURE 1 G) and is shed at the 2-celled stage (FIGURE 1 F). The generative cell is surrounded by a thin sheath of finely granular cytoplasm and a delicate membrane (FIGURE 1 F).

The number of ovules in a carpel varies from 6 to 2 in different genera. They are anatropous, bitegmic, and crassinucellate; the outer integument is vascularized. The hypodermal archesporium is multicellular (FIGURE 1 H) although ultimately only one cell functions. The primary parietal cell divides repeatedly to form the parietal tissue so that the megaspore mother cell is buried deep in the nucellus. At the end of meiosis II linear or T-shaped megaspore tetrads are formed (FIGURES 1 I, J). The chalazal megaspore functions giving rise to the Polygonum type of embryo sac (FIGURE 1 K). The synergids and antipodal cells are ephemeral.

The development of the endosperm is *ab initio* cellular. The first division is transverse and the two chambers thus resulting contribute to the endosperm proper. In *Magnolia obovata* (Kapil & Bhandari, 1964), however, the chalazal chamber gives rise to a 2- or 3-celled haustorium (FIGURE 1 L). The chalazal haustorium is active until the endosperm proper is well developed, but in the ripe seed becomes completely crushed (FIGURE 1 M). The division of the zygote is transverse, obliquely transverse, or vertical (Kapil & Bhandari, 1964). The embryogeny is either irregular or follows the Onagrad type. The mature embryo is dicotyledonous with a prominent suspensor.

The seed coat is organized chiefly from the outer integument while the inner integument is represented by a layer of crushed cells (FIGURE 1 M). In a ripe seed the testa consists of an outer fleshy region comprising (1)

epidermis of the outer integument, (2) 2 or 3 layers of tangentially elongated cells, (3) a 10- to 12-layered fleshy zone, (4) 2 or 3 layers of tangentially compressed cells, and an inner stony region of 3 or 4 layers of lignified cells.

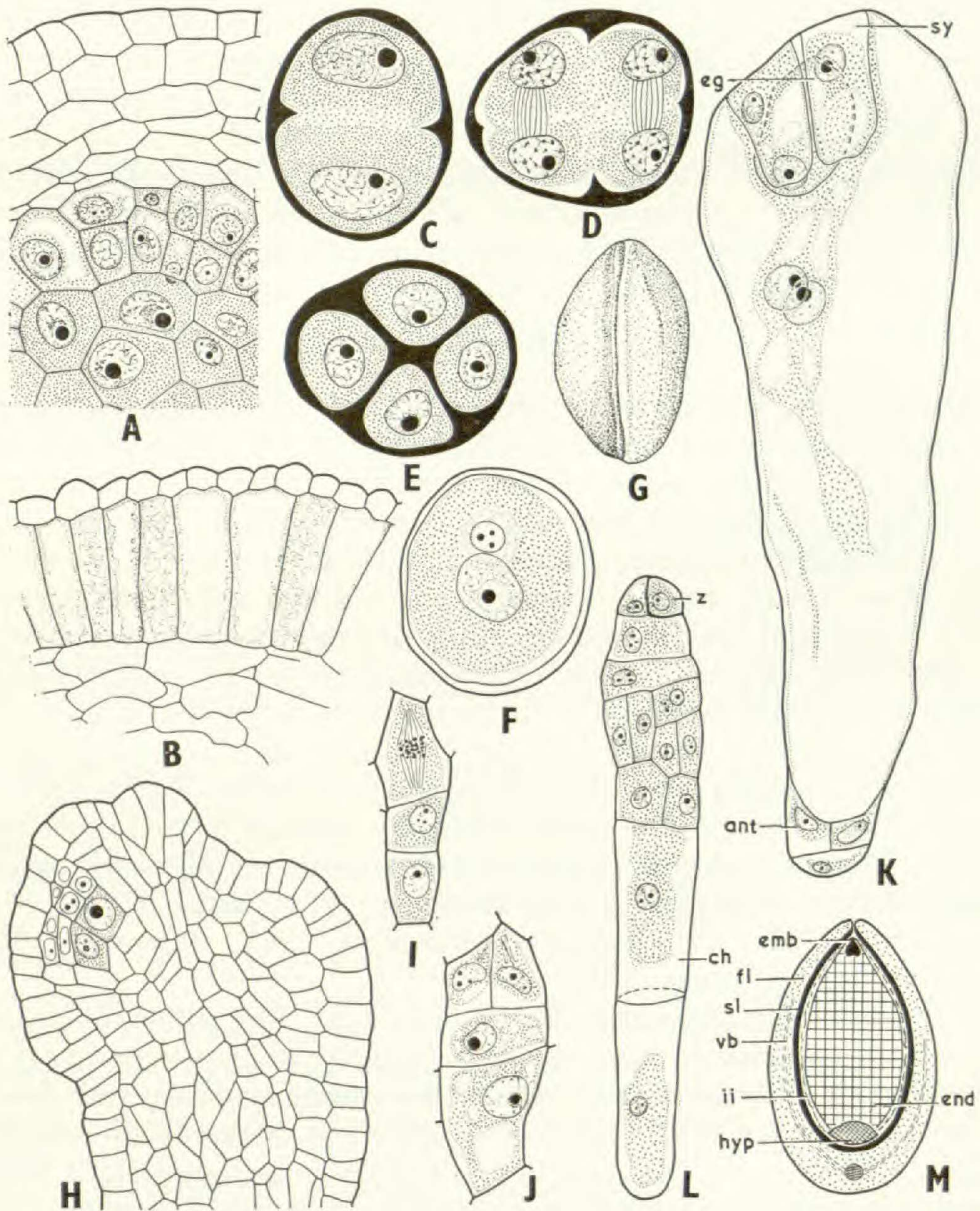


FIGURE 1. Magnoliaceae. (*ant*, antipodal cells; *ch*, chalazal haustorium; *eg*, egg; *emb*, embryo; *end*, endosperm; *fl*, fleshy layer; *hyp*, hypostase; *ii*, inner integument; *sl*, stony layer; *sy*, synergid; *vb*, vascular bundle; *z*, zygote.) A, Transection of a part of the anther lobe showing the wall layers, bilayered tapetum and sporogenous tissue. B, Same, showing reticulate thickening in the endothecium. C-E, Stages in microsporogenesis; cytokinesis occurs by furrowing. F, Two-celled pollen. G, Palynogram. H, Longisection of ovule showing parietal layers, sporogenous tissue and initiation of the two integuments. I, J, Linear and T-shaped tetrads of megaspores. K, Organized embryo sac. L, Linear and T-shaped tetrads of megaspores. M, Longitudinal section of seed showing various zones of testa; chalazal haustorium has degenerated. (A-M, *Magnolia*, after Kapil & Bhandari, 1964.)

A number of stomata of the haplocheilic type develop on the epidermis of the outer integument (*see* Paliwal & Bhandari, 1962).

Cytological investigations (*see* Darlington & Wylie, 1955; Nanda, 1962; Raven, 1967) concern *Liriodendron* (2 spp.), *Manglietia* (2 spp.), *Michelia* (7 spp.), *Pachylarnax phiocarpa*, *Talauma hodgsoni* and *T. phellocarpa*, and *Magnolia* (39 spp.). The basic chromosome number is $x = 19$. Polyploidy is reported in *Magnolia* which includes 4 tetraploid, 11 hexaploid, 1 pentaploid and 1 triploid species. Janaki Ammal (1953) reported $2n = 95$ in *M. soulangeana* whereas Nanda (1962) observed $n = 38$. If the identification of both the plants is dependable, then this is the only record of intraspecific cytological forms. Whatever the origin of basic number, polyploidy seems to have played some role in speciation in *Magnolia*, whereas the chief differences in the genomes seems to have occurred at the gene level within various genera.

Winteraceae. Six vesselless genera with about 95 species comprise the family Winteraceae which is distributed in the tropical and subtropical regions of the world. Three genera are endemic (*Pseudowintera* in New Zealand, *Exospermum* and *Zygonum* in New Caledonia), the other three genera (*Drimys*, *Bubbia*, and *Belliolum*) occur in New Caledonia, New Guinea, eastern Australia, and Central and South America.

The family is of interest because of the presence of a number of primitive characters such as the undifferentiated stamens with protruding connective tissue (*Belliolum*), a conduplicate sessile or stipitate carpel, stigmatic crest, laminar placentation and primitive vesselless xylem. Morphology and anatomy have received adequate attention at the hands of Bailey (1944), Bailey and Nast (1943a,b; 1944a,b; 1945), and Nast (1944). The embryological investigations, however, are restricted to three genera, *Drimys* (Bhandari & Venkataraman, 1968; Kutti Amma, 1938; Strasburger, 1905), *Pseudowintera* (Bhandari, 1963; Sampson, 1963), and *Zygogynum* (Swamy, 1952).

Four groups of archesporial cells (FIGURE 2 A) differentiate in a young anther. The hypodermal layer divides periclinally to form the primary parietal layer and the sporogenous layer; the others, however, add directly to the sporogenous tissue (FIGURE 2 B). The anther wall comprises epidermis, fibrous endothecium, 2 to 4 middle layers and glandular (*Drimys winteri*, *Pseudowintera axillaris*, *Zygogynum*) or amoeboid tapetum (*Pseudowintera colorata*) of parietal origin (FIGURES 2 C, D). The fibrous bands like that of the endothecium extend to 2 or 3 layers of the connective tissue. In *Zygogynum baillonii*, after meiosis is completed in the microspore mother cells, simultaneous cytokinesis results in tetrahedral or decussate tetrads (FIGURES 2 E-H). In *Drimys* and *Pseudowintera* the microspores in the same tetrad show different stages during the formation of the generative cell which is cut off towards the proximal end (FIGURE 2 H), whereas in *Zygogynum* the division is synchronous (FIGURE 2 G). The pollen grains are monoporate; the pore develops at the distal end. The intine is thick and protrudes through the pore. The grains are shed

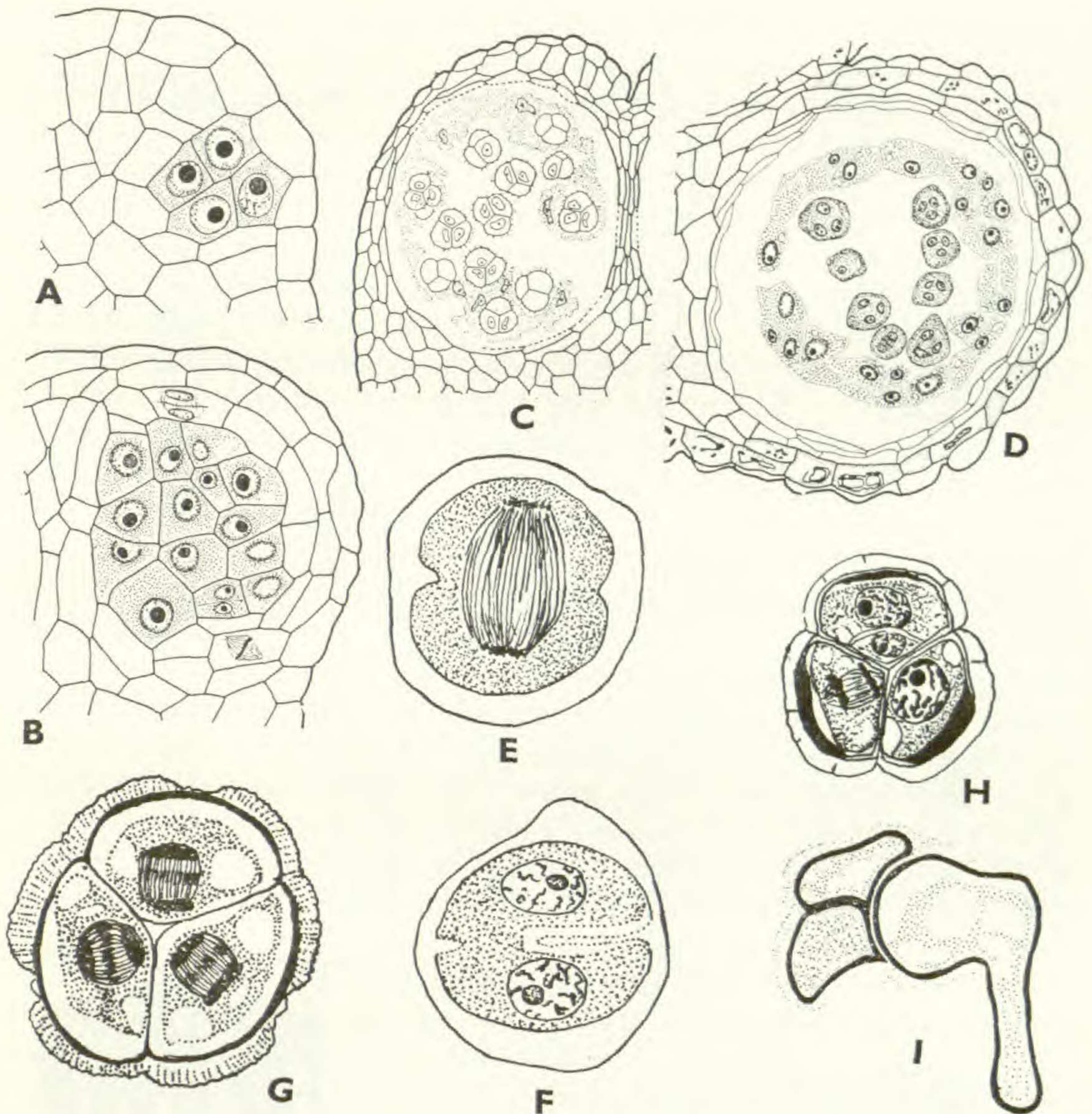


FIGURE 2. Winteraceae. A, Transection of anther showing archesporium. B, Representation of a locule enlarged to show a dividing cell of inner parietal layer which contributes to the tapetum and middle layer II. C, Anther lobe with amoeboid tapetum enveloping the microspore tetrads. D, Anther lobe showing numerous microspore mother cells, surrounding them during meiosis is the detached tapetum. E, Late anaphase of division I. F, After telophase I, note beginning of transverse furrow. G, Simultaneous division of microspore. H, Nonsynchronous division of microspores in a tetrad. I, One pollen grain out of a tetrad germinating. (A, B, D, *Drimys winteri*, after Bhandari & Venkataraman, 1968; C, I, *Pseudowintera colorata*, after Bhandari, 1963; E-G, *Zygogynum baillonii*, after Swamy, 1952; H, *Pseudowintera axillaris*, after Sampson, 1963.)

in permanent tetrads at the 2-celled stage (FIGURE 2 I). In *Zygogynum* (Swamy, 1952) all the pollen grains germinate, while in *Pseudowintera colorata* only one germinates on the stigma; the rest degenerate (FIGURE 2 I).

The ovules are laminar, anatropous, bitegmic, and crassinucellate; the micropyle is formed by the inner integument alone (FIGURE 3 A). A

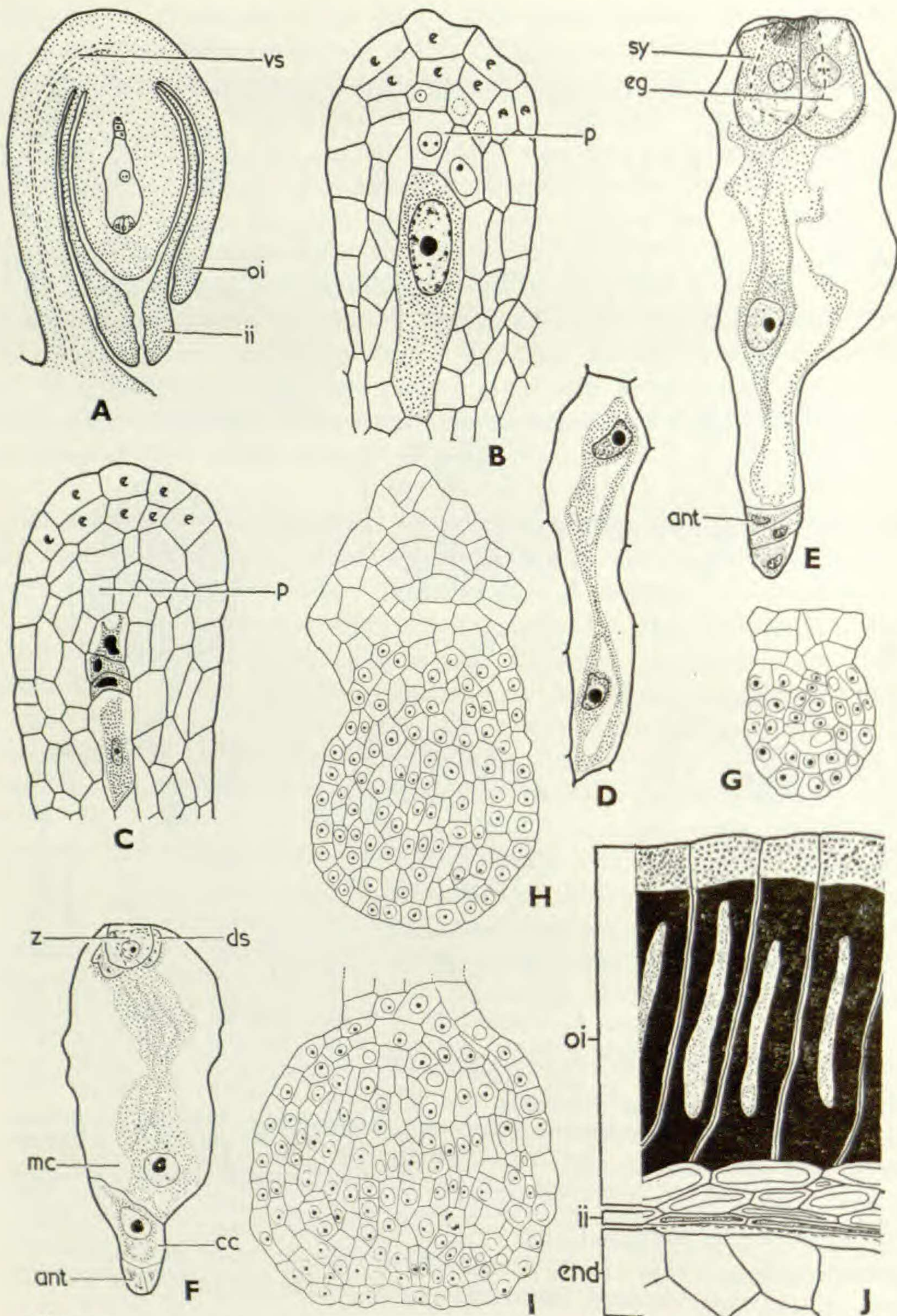


FIGURE 3. Winteraceae. (*ant*, antipodal cells; *cc*, chalazal chamber; *ds*, degenerating synergid; *e*, epidermal cell; *eg*, egg; *end*, endosperm; *ii*, inner synergid; *mc*, micropylar chamber; *oi*, outer integument; *p*, parietal cell; *sy*, mature embryo sac stage. *z*, zygote.) A, Longitudinal section of ovule at mature embryo sac stage. B, Longitudinal section of nucellus showing two-layered parietal tissue and megaspore mother cell. C, Linear tetrad with chalazal megaspore functioning. D, Two-nucleate embryo sac. E, Mature embryo sac, note basal vacuole in the egg also. F, Two-celled endosperm with micropylar and chalazal chambers. G-I, Stages in development of embryo; J, Cross-section of ovule showing integuments (*oi*), endosperm (*end*), and inner integument (*ii*).

single hypodermal archesporial cell divides periclinally to cut off a parietal cell which forms a massive parietal tissue (FIGURE 3 B); the nucellar epidermis may also contribute to the parietal tissue (FIGURES 3 B, C). A linear or T-shaped tetrad is produced at the end of reduction divisions in the megaspore mother cell (FIGURE 3 C). The chalazal megaspore functions to form the Polygonum type of embryo sac (FIGURES 3 C–E). In *Pseudowintera* the synergids have filiform apparatus; the polar nuclei fuse before fertilization and the three small uninucleate antipodal cells are ephemeral (FIGURE 3 E).

Triple fusion precedes syngamy and the endosperm is *ab initio* cellular. In *Pseudowintera* the first division may be transverse (FIGURE 3 F) or vertical. Both the chambers contribute towards the formation of endosperm tissue. The embryogeny has been worked out only in *Drimys* (Bhandari & Venkataraman, 1968) and it is irregular (FIGURES 3 G–I), not conforming to any particular type of Johansen (1950). A suspensor is present but the embryo perhaps remains undifferentiated at the time of shedding of the seeds (FIGURES 3 H, I).

The seed coat is formed chiefly by the outer integument, and the inner becomes almost crushed and is represented by a thin strip of greatly stretched cells (FIGURE 3 J). The cells of the epidermis of the outer integument become elongated, thick walled, brittle, and extremely hard.

The pericarp is about 14–16-layered and remains fleshy and parenchymatous. In *Pseudowintera* meristematic plates of tissue develop in between the maturing seeds so that the fruit becomes chambered. Numerous ethereal oil cells, tannin cells, and stone cells are interspersed in the tissue of the fruit-wall. The pericarp is differentiated into outer tough and coriaceous, and inner spongy, soft regions. The inner region develops numerous ingrowths between the seeds.

Only two genera, *Drimys* and *Pseudowintera* (see Borgamann, 1964; Darlington & Wylie, 1955; Hotchkiss, 1955; Raven & Kyhos, 1965), are known cytologically. In *Drimys* (section TASMANIA) $n = 13$ or 14 has been reported in literature. However, Raven and Kyhos (1965) have shown that reports of $2n = 28$ are erroneous since this number is expressed because of a precocious disjunction in one of the bivalents making the configuration as $n = 12_{II} + 2_I$. Similarly, the count $n = 38$, for *D. winteri* (Whitaker, 1933) has been shown to be erroneous and as reinvestigated by Raven and Kyhos (1965) it is $n = 43$. *Drimys lanceolata* occurs in two cytological races, the diploid with $2n = 26$, and the triploid having $2n = 39$; *Pseudowintera colorata* also shows $n = 43$.

Degeneriaceae. The Degeneriaceae are monotypic and endemic to the Fiji Islands. The family has a number of primitive features such as the

I, undifferentiated heart-shaped embryo contained in a seed obtained from mature fruit. J, Part of seed coat to show crushed and depleted cells of outer and inner integuments; epidermis of radially elongated outer integument constitutes major part of seed coat. (A–F, J, *Pseudowintera colorata*, after Bhandari, 1963; G–I, *Drimys winteri*, after Bhandari & Venkataraman, 1968.)

broad laminar stamens (without any differentiation into filament, connective, and anther) having four microsporangia embedded on the abaxial surface; conduplicate carpel devoid of any style and stigma, and instead, having a decurrent stigmatic crest; laminar ovules; multilacunar node; and a primitive type of wood.

Swamy (1949) has worked out the embryology, and Dahl and Rowley (1965) the ultrastructure of pollen of *Degeneria vitiensis*. In a young anther four groups of archesporium differentiate (FIGURE 4 A). The wall of the anther on the abaxial surface comprises an epidermis, 1-layered fibrous endothecium, three or four middle layers, and a single-layered tapetum with binucleate cells (FIGURES 4 B, C). At the time of dehiscence only the epidermis and endothecium persist; towards the connective region some more layers develop thickenings like that of the endothecium. The cytokinesis is simultaneous and results in tetragonal tetrads (FIGURE 4 D). The germinal furrow begins to develop on the distal end even when the microspores are in tetrads (FIGURES 4 D, F). The generative cell is cut off towards the distal end (FIGURE 4 E). The pollen grains are monocolpate and 2-celled at the shedding stage.

There are nearly 30 to 32 ovules in a carpel. They are laminar, anatropous, bitegmic and crassinucellate. The micropyle is formed by the inner integument alone (FIGURE 4 I); a funicular obturator is very conspicuous and is comprised of elongated and densely cytoplasmic cells of the epidermis. The 1-celled archesporium is hypodermal and a massive tissue is formed by the primary parietal cell (FIGURE 4 H). A linear tetrad is produced, of which the chalazal megaspore (FIGURE 4 I) functions to form the Polygonum type of embryo sac (FIGURE 4 J). The synergids and the antipodal cells are short-lived.

After pollination, when the pollen grains fall on the stigmatic surface, they germinate and the pollen tube is put forth from one of the two broader ends of the germinal furrow (FIGURE 4 G). Triple fusion precedes syngamy and the endosperm is *ab initio* cellular (FIGURE 4 K). The mature endosperm is ruminant (FIGURE 4 T). The zygote divides only after a massive endosperm tissue is formed (FIGURE 4 L). Although the first division of the zygote is transverse; subsequent segmentation does not follow any strict pattern (FIGURES 4 M-Q). However, the process of tissue differentiation later becomes quite stabilized. The mature embryo is either tri- or tetracotyledonous having a short suspensor, a bulbous hypocotyl, and well differentiated cotyledons (FIGURES 4 R, S).

The seed coat is formed by the outer vascularized integument whereas the inner integument becomes reduced to a membranous layer of crushed cells. The testa is differentiated into an outer succulent region with numerous groups of oil cells and an inner ridged stony region enclosing the ruminant endosperm (FIGURES 4 T, U).

Recently Raven and Kyhos (1965) reported $n = 12$ for the monotypic family and that, therefore, constitutes the basic haploid number. The karyotype has not been investigated.

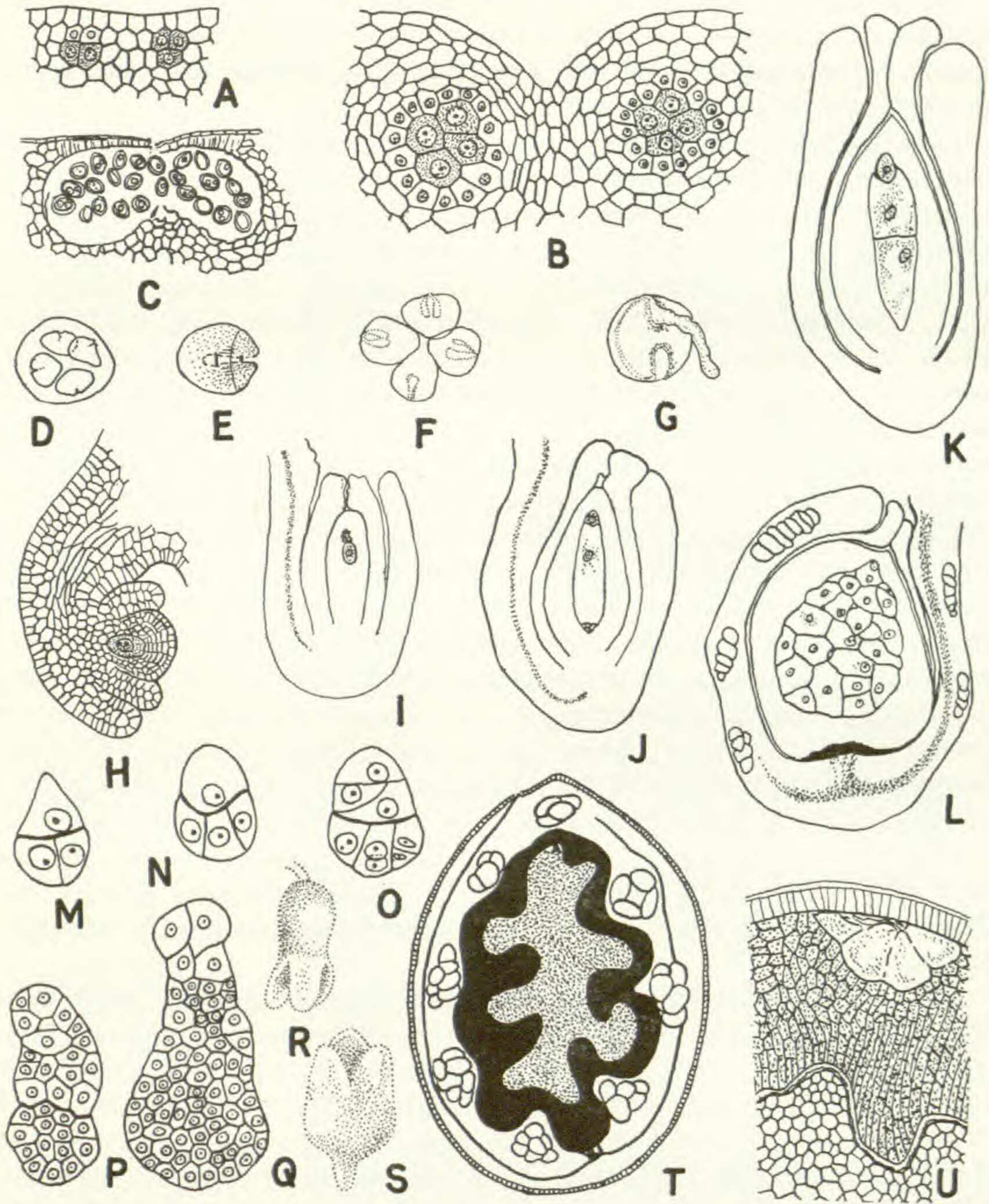


FIGURE 4. *Degeneriaceae*. A, Part of transverse section of anther showing two groups of archesporium. B, Same, showing differentiation of wall layers. C, Two adjacent microsporangia after dehiscence showing two-celled pollen grains. D, Tetragonal tetrad of spores. E, Microspore showing formation of the generative cell. F, Tetrad showing development of colpi in microspores. G, Germinating pollen grains. H, Longitudinal section of ovule showing megaspore mother cell and parietal tissue. I, Same, showing linear tetrad of which chalazal megaspore is functional. J, Same, showing mature embryo sac. K, Two-celled endosperm. L, Longitudinal section of developing seed, showing massive endosperm and zygote. M-Q, Stages in development of embryo. R, S, Tricotyledonous embryos showing suspensor, hypocotyl, and cotyledons. T, Longitudinal section of mature seed showing outer fleshy and inner stony regions, ruminant endosperm, and small embryo. U, Part of seed coat enlarged from FIGURE T. (A-T, *Degeneria vitiensis*, after Swamy, 1949.)

Annonaceae. The Annonaceae is the largest of all the woody magnolian families and comprises 120 genera with approximately 2,100 species. The family is cosmopolitan and well represented in tropical and subtropical to temperate regions of the world.

Only one tenth of the total number of genera and about 15 species have been worked out embryologically. In a young anther the archesporium is either multicelled as in *Artabotrys* (Asana & Adatia, 1947) and *Miliusa* (Periasamy & Swamy, 1959), or it is differentiated as a uniseriate row (FIGURE 5 A) in *Annona* (Juliano, 1935), *Cananga* (Periasamy & Swamy, 1959), *Asimina* (Locke, 1936), *Monodora* and *Xylopia* (Lecomte, 1896). In the latter group of plants some of these cells form sterile septae (FIGURE 5 D) so that individual microspore mother cells or a group of them become separated (Juliano, 1935; Periasamy & Swamy, 1959). The tapetum along the protruding part of the microsporangium is parietal in origin (FIGURES 5 B, C). The anther wall is constituted of the epidermis, the fibrous endothecium, and three or four middle layers (FIGURE 5 F). The tapetum is glandular as in *Artabotrys*, *Cananga*, and *Miliusa* or amoeboid as in *Annona* (Juliano, 1935; Asana & Adatia, 1947), *Polyalthia*, *Unona*, and *Cananga* (see Asana & Adatia, 1947). Cells of the tapetum are binucleate or tetranucleate, or the four nuclei fuse to form a tetraploid nucleus (FIGURE 5 E). In *Cananga odorata* (Periasamy & Swamy, 1959), *Asimina* (Herms, 1907), and *Annona* (Juliano, 1935) the tissue of the sterile septae in the microsporangium behave as the tapetum (FIGURE 5 D) and therefore, it may be regarded that tapetum is being contributed by the parietal as well as the sporogenous tissues. In the light of Periasamy and Swamy's (1959) observations on *Cananga* and *Miliusa*, the genera reported to have amoeboid tapetum need a reinvestigation.

The process of cytokinesis is successive in *Annona* (Juliano, 1935; Sastri, 1957) and *Uvaria* (Sastri, 1957) but simultaneous in *Cananga* (Periasamy & Swamy, 1959), *Annona* (Samuelson, 1914), *Asimina* (Locke, 1936), *Polyalthia*, and *Saccopetalum* (Sastri, 1957). In *Cananga* and *Miliusa* the first furrow starts at the end of heterotypic division but is completed along with the second at the termination of homotypic division (FIGURES 5 G, H). The microspore tetrads are tetrahedral, tetragonal, or decussate. In *Annona* the pollen grains remain in permanent tetrads. At the time of shedding the pollen grains are 2-celled (FIGURE 5 J), the generative cell being cut off towards the distal end (FIGURE 5 I); they are monocolpate or acolpate (rarely with a slit-like aperture as in Magnoliaceae); and the exine is psilate, verrucate, reticulate, or even echinate (see Erdtman, 1952).

The ovules are anatropous, bitegmic, tritegmic (FIGURE 6 B) and crassinucellate. The micropyle, however, is formed by the outer or inner integument or by both, the middle remains rather arrested (FIGURE 6 B). The outer integument is vascularized as in some Magnoliaceae. In *Cananga odorata* (Periasamy & Swamy, 1956) and *Saccopetalum tomentosum* (Sastri, 1957) the carpel is conduplicate and the ovules receive their vasculari-

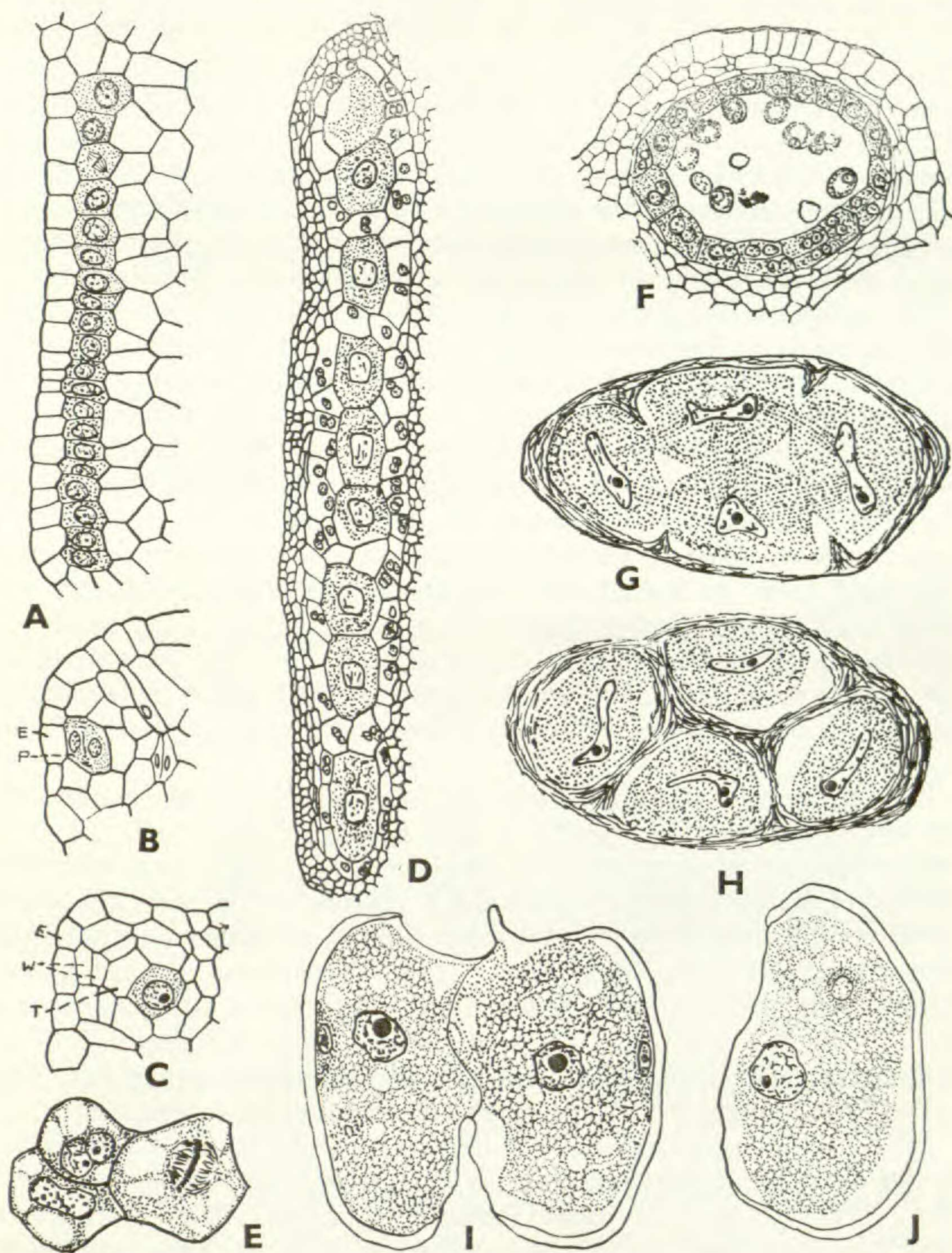


FIGURE 5. Annonaceae. (*e*, epidermis; *p*, parietal layer; *t*, tapetum; *w*, wall layers.) A, Longitudinal section of a young anther locule showing uniseriate row of archesporial cells. B, C, Transverse sections of stamens showing successive stages in development of wall layers. D, Longitudinal section of anther locule showing sterilization of sporogenous cells and formation of sterile septa. E, Behavior of nuclei of tapetal cells. F, Transverse section of anther showing wall layers, tapetum and microspores. G, H, Stages in cytokinesis by furrowing. I, Two-celled pollen grains soon after division of microspore nucleus. J, Two-celled pollen; generative cell with granular cytoplasm surrounded by hyaline membrane. (A-J, *Cananga odorata*, after Periasamy & Swamy, 1959.)

zation by the traces from the dorsal bundles. A hypostase has been reported in *Asimina* and *Artabotrys*. An aril is present in some members (Corner, 1948). The hypodermal archesporium is 1- to few-celled (FIGURE 6 A), and the massive parietal tissue is formed by the primary parietal cell (FIGURE 6 B). At the end of meiosis I a dyad is formed (FIGURE 6 B) which results in a linear tetrad, of which the chalazal megaspore functions (FIGURE 6 C). The development of the female gametophyte conforms to the *Polygonum* type. The synergids are hooked and the antipodal cells remain uninucleate (FIGURE 6 D). The synergids and 3 small antipodal cells degenerate immediately after fertilization.

The endosperm is cellular. The first and the following few divisions in the endosperm are transverse so that a uniseriate row of endosperm cells is formed (FIGURE 6 E, F). Later the endosperm becomes massive and ruminant (FIGURE 6 K). The zygote divides transversely (FIGURE 6 G), followed by vertical division in the resulting two cells. In *Polyalthia longifolia* (Sastri, 1955a) the derivatives of the basal cell give rise to hypophysis and suspensor, whereas the derivatives of the terminal cell form two piers, upper *pc* forming the central cylinder of stem and cotyledons, and lower *pc* contributing entirely to the hypocotyledonary regions. In *Cananga odorata* (Periasamy & Swamy, 1961), the basal cell undergoes a transverse division (FIGURES 6 H, I). The derivatives of the octants form a globular embryo (FIGURE 6 J) which differentiates later into a dicot embryo. The embryogeny, therefore, follows the *Trifolium* or *Lotus* variation of the *Onagrad* type.

The seed coat is formed chiefly by the outer integument alone, although the inner integument may persist in some genera (FIGURES 6 K, L). The ruminations, which are produced by the outer integument, are pushed into the developing endosperm (FIGURE 6 L). During this process the tissue of the nucellus and the inner integument become compressed and line the ingrowths of the outer integument. These ruminations are not vascularized. A poorly or a well-developed aril is present in the annonaceous seeds (FIGURE 6 K). The ripe seeds have copious endosperm with or without starch (Corner, 1948) and a small dicotyledonous embryo. Occasionally composite fruits (syncarps) are produced, as in *Annona*.

Out of 120 genera only 15 have been worked out cytologically (Darlington & Wylie, 1955; Mangenot & Mangenot, 1957, 1958; Mangenot *et al.*, 1957; Miège, 1954, 1960; Pawar *et al.*, 1956). Of these, 8 genera have $x = 8$, 3 have $x = 9$, and two have $x = 7$. *Rollinia orthopetala* shows $n = 24$ which according to Darlington and Wylie (1955) may be doubtful. Only *Artabotrys odoratissimus* has forms with $n = 8$ or 9, while *Asimina triloba* is found to be either diploid, with $2n = 18$, or triploid, $2n = 27$. Therefore, the family is characterized by three basic numbers, $x = 7, 8$, and 9. Since a larger number of genera and species possess $x = 8$, it is likely that the other genera evolved by addition or subtraction of one chromosome, or by a multiple of this base number.

Myristicaceae. The Myristicaceae include 15 genera and nearly 250 species which are met with in new world tropics, Africa, and Asia. Vas-

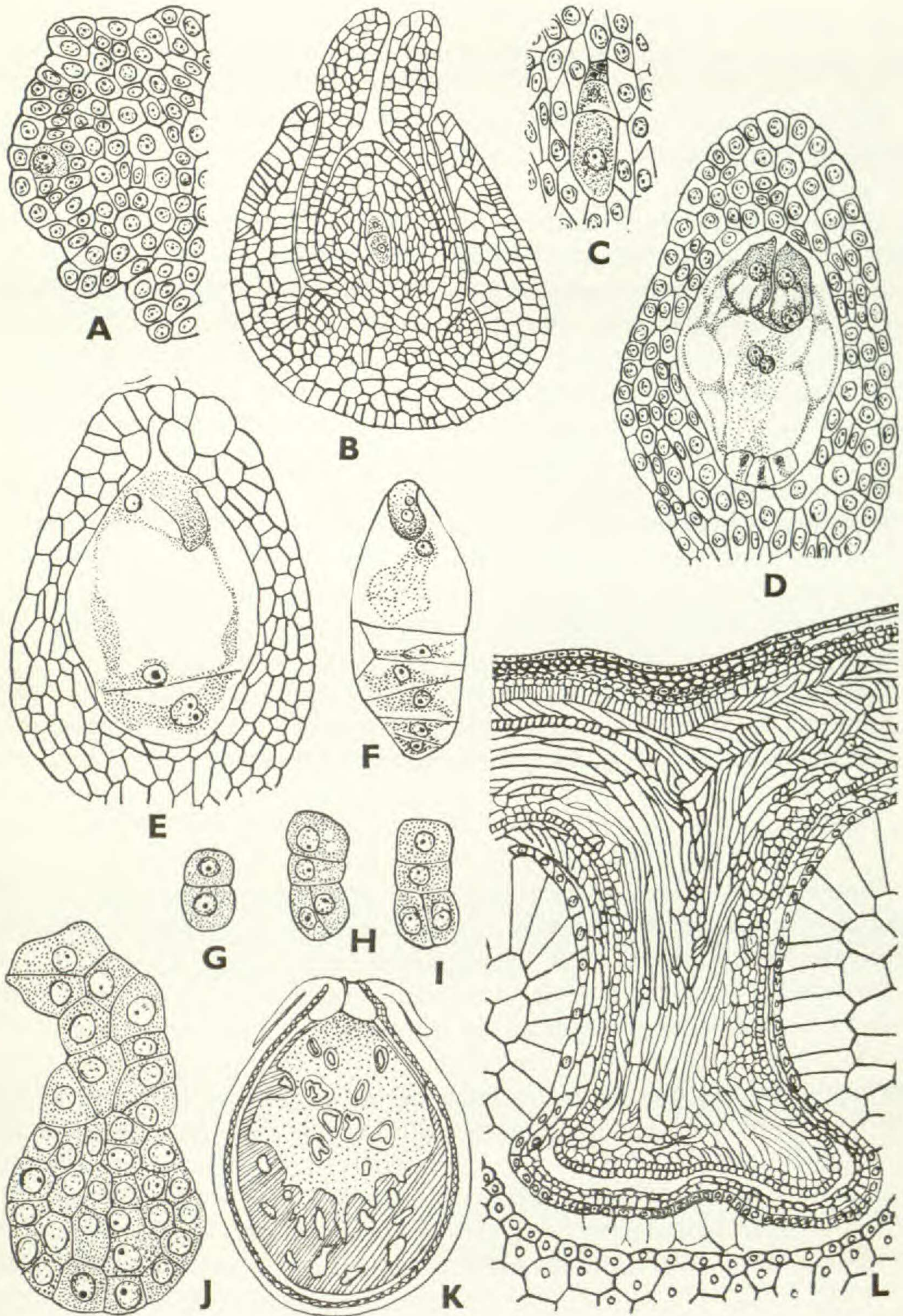


FIGURE 6. *Annonaceae*. A, Longitudinal section of ovule showing hypodermal archesporial cell and origin of integuments. B, Transmedian longitudinal section of the ovule just after the initiation of the middle integument. C, Linear tetrad, the three micropylar megaspores degenerating. D, Mature embryo sac. E, Longitudinal section of 2-celled endosperm and nucellus. F, Longitudinal section of young endosperm showing linear series of cells with a larger micropylar one. G-J, Stages in embryogenesis. K, Median longitudinal section of seed at the time when endosperm expands rapidly. L, Fully formed rumination process with nucellar remains and endosperm in immature seed. (A-L, *Cananga odorata*, after Periasamy & Swamy, 1961.)

cular anatomy of the flower, aril, and embryology of only *Myristica* spp. has been worked out (Camp & Hubbard, 1963; Joshi, 1946; Nair & Bahl, 1956; Nair & Pillai, 1959; Periasamy, 1961; Sastri, 1955b).

The anther wall is composed of epidermis, fibrous endothecium, two ephemeral middle layers, and a single-layered glandular tapetum comprising uninucleate cells. At the end of meiosis the successive type of cytokinesis in the microspore mother cells results in isobilateral tetrads. The pollen grains are 2-celled and 1-sulcate.

The anatropous ovules are bitegmic and crassinucellate; the micropyle is constituted by the inner integument. A single archesporial cell cuts off a parietal cell which by periclinal and anticlinal divisions forms a massive parietal tissue. The megaspore mother cell is deeply buried and forms a linear tetrad at the end of meiosis. The chalazal megaspore is functional which gives rise to the Polygonum type of embryo sac.

The endosperm is nuclear and later becomes cellular and ruminant. The embryo development has not been worked out. The seed coat is formed by the outer integument whereas the ruminations are developed from the massive tissue formed by the meristematic chalazal region (Periasamy, 1961). The aril which develops from the outer integument is vascularized and forms a network covering the mature seed.

Only *Myristica fragrans* (Simmonds, 1954) and *Pycnanthus angolensis* (Mangenot & Mangenot, 1957) have been worked out and these show $n = 21$ and $n = 19$, respectively. The basic number is doubtful and may turn out to be $x = 7$ but requires more intensive work before anything can be finally said.

Canellaceae. The family Canellaceae comprises six genera and 20 species distributed disjunctively from Venezuela to southern Florida, tropical America, Puerto Rico, Madagascar, and tropical Africa.

Parameswaran's (1961, 1962) is the only embryological account available for *Canella alba* and *Warburgia stuhlmannii*. The androecium of the family is syngenesious. The paired anther thecae arise in the form of longitudinal ridges i.e. protuberant columns of cells. At the outer corners of the column hypodermal archesporial cells become differentiated, then divide periclinally to form the primary parietal cell and the sporogenous cells (FIGURE 7 A). The primary parietal cell forms 5-layered tissue, of which the innermost forms the glandular tapetum, the next 2 or 3 layers are the middle layers, while the outer gives rise to the fibrous endothecium (FIGURE 7 B). The tapetal cells become bi- or tetranucleate after which the nuclei fuse to form a tetra- or octoploid nucleus. In *Canella alba* and *Warburgia stuhlmannii* the inner wall of the tapetum becomes studded with minute protuberances (Ubisch granules) along its inner and outer surfaces (FIGURE 7 E). In the dehisced anther the wall is comprised of only the persisting protuberant epidermis and fibrous endothecium; the rest of the layers degenerate (FIGURE 7 C). The microspore mother cells produce tetrahedral tetrads after meiosis (FIGURE 7 F). The generative cell is cut off towards the proximal pole even before the pollen grains are

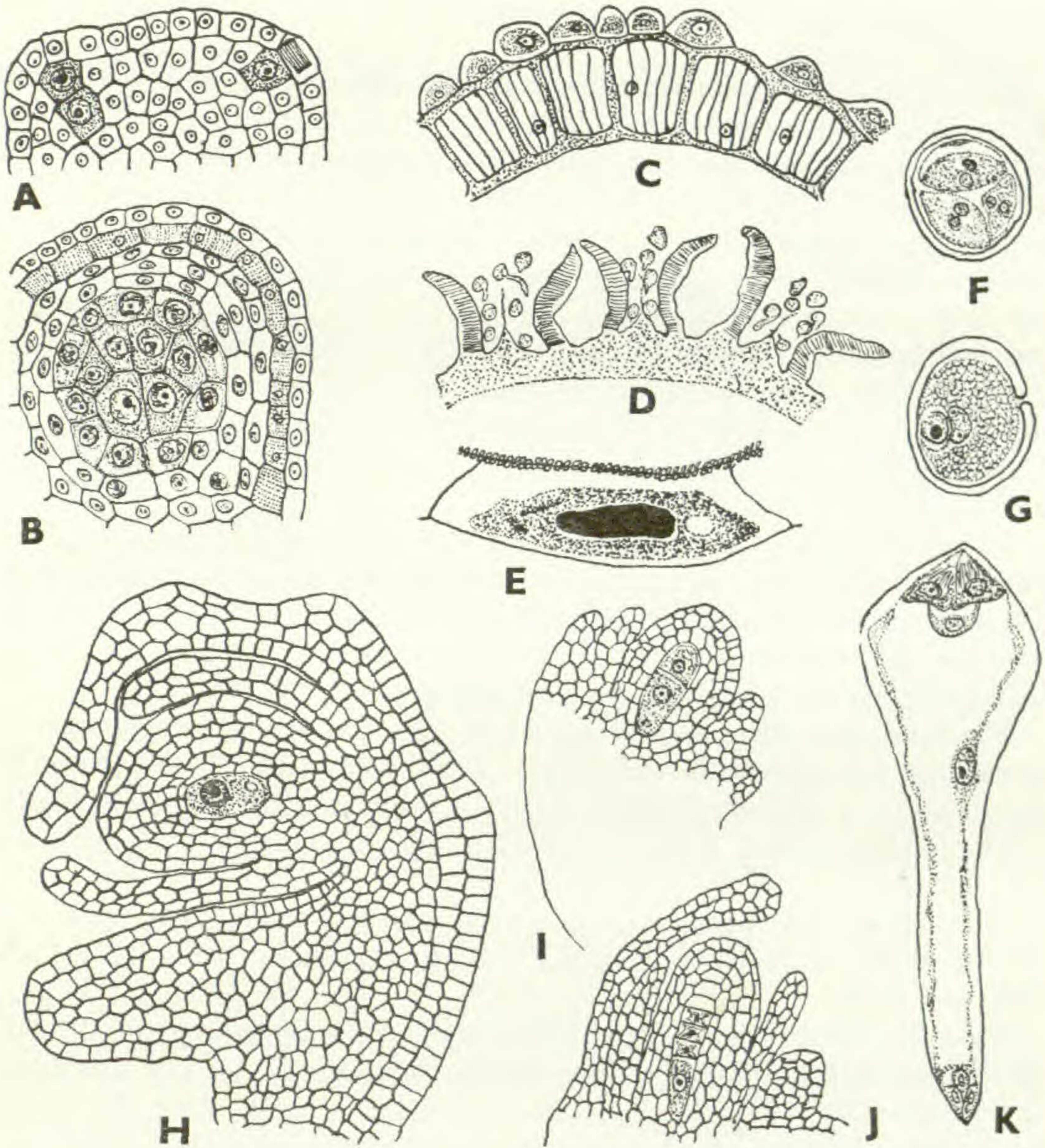


FIGURE 7. *Canellaceae*. A, Transection of sector of young anther primordium showing archesporial cell has divided into primary parietal and sporogenous cells. B, Same, showing epidermis, endothecium, three wall layers, tapetum, and group of microspore mother cells. C, Endothecium and persisting epidermis. D, Germinating pollen grain, lodged in dehiscid anther thecae. E, Tapetal cell showing ubiquinone granules along both surfaces of tangential wall. F, Microspore tetrad after division of microspore nucleus into generative and vegetative cells. G, Sectional view of mature 2-celled pollen showing germinal furrow. H, Longitudinal section of young ovule containing megaspore mother cell. I, Dyad stage. J, Linear tetrad—note accelerated growth of outer integument at one side. K, Mature embryo sac. (A–G, K, *Canella alba*; H–J, *Warburgia stuhlmanii*, after Parameswaran, 1962.)

released from the tetrads (FIGURE 7 F). A large number of pollen grains germinate *in situ* (FIGURE 7 D), and in such germinated pollen the sperm and the elongated vegetative nucleus occupy the terminal part of the pollen tube. The pollen grains are monocolpate (FIGURE 7 G) and the col-

pus develops along the distal pole concurrently with division of the microspore nucleus.

The ovules are hemianatropous, bitegmic and crassinucellate (FIGURE 7 H). The two integuments differentiate simultaneously but the outer grows faster and asymmetrically on the antiraphe side (FIGURE 7 H, J). The micropyle is zigzag and is constituted by both the integuments. The hypodermal archesporium is 1-celled. The primary parietal cell forms a massive parietal tissue (FIGURE 7 H) so that the female gametophyte lies deeply buried in the nucellus. In *Warburgia* a linear tetrad of megaspores is formed, of which the chalazal functions (FIGURES 7 I, J) to form the Polygonum type of female gametophyte. The synergids have a conspicuous filiform apparatus, the polar nuclei fuse before fertilization and 3 uninucleate antipodal cells are organized (FIGURE 7 K). Both the antipodals and the synergids are ephemeral.

The development of endosperm has not been worked out; however, Parameswaran (1961) has recorded ruminant endosperm in *Cinnamosma*. The ruminations formed by the seed coat are nonvascularized. The embryogeny is unknown but the mature seed contains a slightly curved embryo embedded in a copious oily endosperm tissue.

The inner and outer epidermis of the inner and outer integuments respectively, constitute the seed coat. The epidermal cells of the outer integument are infiltrated with some black contents, and become sclerotic.

The family has $n = 11$ or 13 , and these may also be the basic numbers.

Illiciaceae. Illiciaceae is a monogeneric family comprising nearly 42 species which are met with in China, Japan, Indochina, West Indies, Sikkim, and India.

Hayashi (1960, 1963) has investigated the embryology of *Illicium floridanum* and *I. anisatum*. The anther wall constitutes the epidermis, the endothecium which develops fibrous thickenings after the pollen grains have been formed, 2 or 3 middle layers, and the irregularly 2-layered glandular tapetum. The cells of the tapetum are considered to have originated from the sporogenous tissue surrounding the microspore mother cells. Critical stages to justify the sporogenous origin of the tapetum are, however, wanting. At the end of meiosis II, simultaneous cytokinesis results in tetrahedral tetrads. The pollen grains are isopolar, tricolporate and 2-celled at the time of shedding.

The ovules are anatropous, bitegmic, and crassinucellate. The female archesporium is single-celled. The parietal cell divides anticlinally as well as periclinally and forms a massive parietal tissue resulting in a deeply buried megaspore mother cell. The chalazal megaspore of a linear tetrad gives rise to a Polygonum type of female gametophyte. The three uninucleate antipodal cells are ephemeral.

The development of endosperm is *ab initio* cellular (Hayashi, 1963). Earle's (1938) report of nuclear endosperm seems to be erroneous. The development of the embryo conforms to the Asterad type. Recently Stone and Freeman (1968) have worked out the cytotaxonomy of two species of *Illicium*, *I. floridanum* and *I. parviflorum* and found that the former

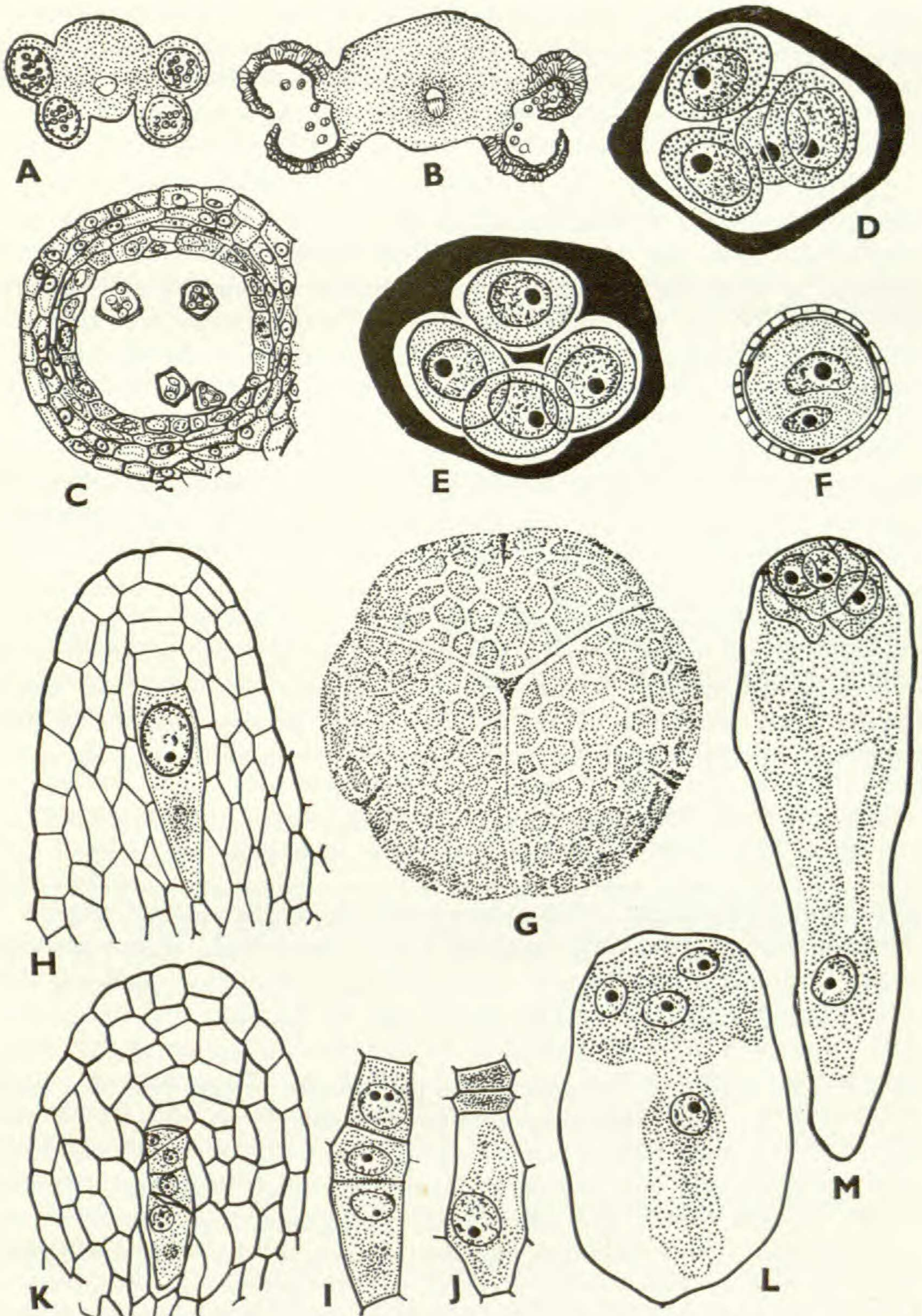


FIGURE 8. Schisandraceae. A, B, Transverse sections of anther at the microspore and 2-celled stage of pollen grain; in B note irregularly 1- or 2-layered fibrous endothecium. C, Anther locule to show wall layers. D, E, Tetrahedral and decussate microspore tetrads. F, Two-celled pollen grain. G, Pollen grain with a triradiate mark formed by meeting of three furrows; exine is reticulate. H, Longitudinal section of nucellus showing parietal cells and megaspore mother cell. I, Triad. J, Functioning megaspore, degenerated upper dyad cell, and middle non-functioning megaspore. K, A tetrad of megaspores. L, Four-nucleate embryo sac. M, Mature female gametophyte. (A-J, L, M, *Schisandra grandiflora*, after Kapil & Jalan, 1964; K, *S. chinensis*, after Swamy, 1964.)

has $n = 13$ whereas the latter possesses $n = 14$. They suggest that Whitaker's (1933) report of *I. floridanum* and *I. anisatum* (*I. religiosum*) as having $n = 14$ is, perhaps, incorrect. They explain the origin of $n = 13$ in *I. floridanum* by aneuploidy from $n = 14$ of *I. parviflorum*.

Schisandraceae. Two genera of woody vines, *Schisandra* and *Kadsura*, comprise the family Schisandraceae which is distributed in eastern and southeastern Asia and Malesia. Only *Schisandra glabra* is a native of America. In India there are four species found in the eastern and western Himalayas. In the Schisandraceae amongst many characters, the formation of a modified column by the basal connation of the filaments of the stamens, the conduplicate carpel with ventral stigmatic crest, and its distal extension to form a non-vascularized pseudostyle are of interest.

The anther wall comprises a persistent epidermis, 1- or 2-layered fibrous endothecium, 2 or 3 middle layers, and irregularly bilayered glandular tapetum (FIGURES 8 A-C). As the anther matures the epidermal cells become papillate and several of these become packed with tannin. The endothecium develops vertically oriented fibrous thickenings whereas the middle layers degenerate soon after the reduction divisions are completed. The cells of the tapetum become multinucleate, and the nuclei fuse to form polyploid masses. At the time of dehiscence, the epidermis, endothecium, and remnants of the middle layers persist (FIGURE 8 B). Numerous ethereal oil cells are present in the connective tissue. The cytokinesis is simultaneous, resulting in tetrahedral and decussate tetrads (FIGURES 8 D, E). The pollen grains are tri- or hexacolpate (FIGURE 8 G). The latter have three small and three large meridionally arranged furrows. The large colpi fuse at one end to form a triradiate mark (FIGURE 8 G). The pollen grains are shed at the 2-celled stage (FIGURE 8 F).

The ovules are anatropous, bitegmic, and crassinucellate. Both the integuments organize the micropyle. A single hypodermal cell cuts off a primary parietal cell which divides periclinally to produce 3 or 4 parietal cells (FIGURE 8 H). In *Schisandra grandiflora* (Kapil & Jalan, 1964) after a dyad is formed, the lower dyad cell divides to give rise to a triad (FIGURE 8 I). The chalazal megaspore functions (FIGURE 8 J) to produce the Polygonum type of embryo sac (FIGURES 8 L, M). The antipodal cells are ephemeral and degenerate soon after their inception (FIGURE 8 M). Yoshida (1962) also reported the Polygonum type of embryo sac in *S. chinensis*. In *S. chinensis*, however, Swamy (1964) reported monosporic as well as bisporic development of the embryo sac (FIGURES 8 K; 9 A, B), and according to him the organization of the mature embryo sac is accomplished after the 4-nucleate stage (Oenothera type). The antipodal cells and one of the polar nuclei are lacking. So far no bisporic embryo sac with such an organization has been recorded. Keeping in view the divergent interpretation concerning the development of the female gametophyte, a reinvestigation is much desired.

The pollen grains are monosiphonous, fertilization is porogamous and one or both the synergids become crushed during this process. The endo-

sperm is cellular. The first division is transverse and results in a large micropylar and a small chalazal chamber (FIGURE 9 C). Further growth in both the chambers results in a massive endosperm tissue which fills almost the entire cavity of a mature seed (FIGURES 9 D, E). The division of the zygote is either transverse or vertical (FIGURES 9 F, G). The derivatives of *ca* form the octant having 4 cells in tier 1' and 1 (FIGURES 9 H–J). Embryogeny follows the Asterad or Onagrad type. The mature embryo is dicotyledonous (FIGURE 9 E).

The seed coat is contributed by both the integuments, the outer integument comprising an epidermis of macrosclereids, 2 or 3 subepidermal layers of brachysclereids, followed by 2 or 3 layers of parenchymatous tissue; whereas the inner integument persists as a thin 2-layered tissue of thick-walled cells (FIGURE 9 K). The fruit wall is fleshy and succulent and comprises 14 to 16 layers of enlarged parenchymatous cells. There are numerous ethereal oil cells interspersed in the outer epidermis of the pericarp.

The two genera, *Schisandra* and *Kadsura*, of the family Schisandraceae possess $n = 14$ (Darlington & Wylie, 1955; Stone, 1968). The basic number was thought by Darlington and Wylie (1955) to be $x = 7$. According to Stone (1968) the karyotype is different from that of Illiciaceae in being nearly symmetrical and showing an absence of subterminal chromosomes.

Monimiaceae. In the Monimiaceae there are about 34 genera and 450 species met with in tropical and subtropical regions with distributional centers in Australia, Polynesia, Madagascar, tropical Africa, South America, and Mexico.

Of the larger number of genera and species, the embryology of only *Peumus boldus* (Mauritzon, 1935) has been worked out in detail, in addition to some fragmentary information that exists on *Siparuna eggersii* (Heilborn, 1931) and *Mollinedia* (Peter, 1920). The anther wall comprises epidermis, fibrous endothecium, 2 or 3 middle layers, and a 1-layered glandular (periplasmodial in *Atherosperma*, see Sastri, 1963) tapetum. At the end of meiosis, tetrahedral tetrads of microspores are formed by simultaneous cytokinesis. The pollen grains are shed individually or they remain in permanent tetrads in *Hedycarya angustifolia* (Money, Bailey, & Swamy, 1950). They are mono-, bi-, or acolpate and are shed at the two-celled stage.

The ovules are anatropous unitegmic (*Siparuna*) or bitegmic (*Peumus boldus*) and crassinucellate. The micropyle in *Peumus* is formed by both the integuments. The nucellar epidermis at the tip undergoes periclinal divisions (FIGURE 10 F) so that a 4–6-layered nucellar cap is formed. At the mature embryo sac stage a conspicuous hypostase is present. The female archesporium is multicelled in *Siparuna* but is one-celled in *Peumus* (FIGURES 10 A, F). The archesporial cell forms the primary parietal cell which divides repeatedly to result in a massive parietal tissue so that the megaspore mother cell is deeply buried in the nucellus (FIGURES 10 A, F).

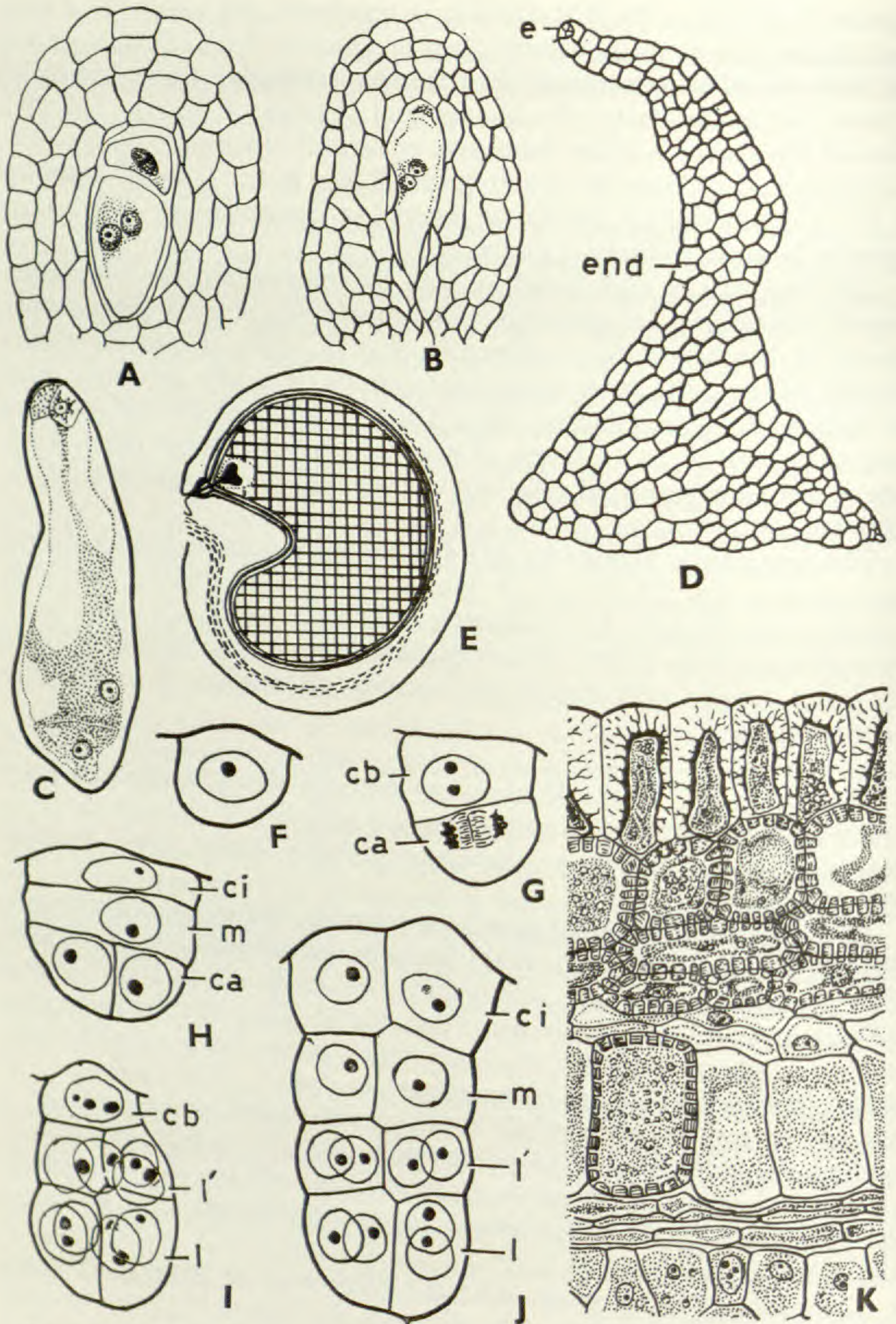


FIGURE 9. Schisandraceae. (*e*, embryo; *end*, endosperm.) A, Chalazal dyad cell with two megaspore nuclei and micropylar dyad cell in meiosis II. B, Micropylar dyad cell degenerating and chalazal cell with two megaspore nuclei. C, Two-celled endosperm. D, Endosperm at 4-celled stage of embryo. E, Longisection of seed at dicotyledonous stage of embryo. F, Development of embryo. K, Part of seed coat showing macrosclereids, brachysclereids, and other layers of testa. (A, B, *Schisandra chinensis*, after Swamy, 1964; C-K, *S. grandiflora*, after Kapil & Jalan, 1964.)

After meiotic division in the megaspore mother cell a linear tetrad is formed in *Siparuna* and *Mollinedia* (FIGURE 10 A). In *Siparuna* the chalazal megaspore functions and forms a long, tortuous chalazal tube with a vesicular tip (FIGURES 10 A, B). The tip of this tube bursts into another cell and discharges its contents (FIGURE 10 C). It forms a 4- or 5-nucleate female gametophyte that remains unorganized in *Siparuna*. However, in *Mollinedia* a normal embryo sac is formed. On the other hand, in *Peumus*, cytokinesis is suppressed after meiosis II, and subsequently the upper of the two dyad cells degenerates (FIGURE 10 G), whereas the lower functions to form the embryo sac (FIGURE 10 H). The development of the embryo sac is, therefore, of the *Polygonum* and *Allium* types. An antipodal complex of 5 to 20 cells is observed in *P. boldus* (FIGURE 10 I, J).

The development of endosperm is cellular. The first division is transverse which divides the embryo sac into a large micropylar and a much smaller chalazal chamber. The next division in the chalazal chamber is vertical and is followed by a few transverse divisions in the micropylar chamber (FIGURE 10 R). By repeated divisions both the chalazal and micropylar chambers form a massive endosperm tissue (FIGURE 10 S).

The zygote divides transversely (FIGURE 10 K) to form the cells *ca* and *cb*. Subsequently these two cells undergo either transverse or vertical division (FIGURES 10 L, M) or the cell *ca* may divide transversely whereas the cell *cb* divides vertically (FIGURE 10 N), indicating that there is a lot of plasticity in the pattern of divisions during early embryogeny. Later however, the derivatives of the *ca* form the embryo proper while those of the *cb* form a short suspensor (FIGURE 10 Q, R). In the mature seed there is a small embryo embedded in a copious endosperm. According to Johanson (1950), the embryogeny conforms to the Asterad type.

It must be realized that the foregoing embryological account is based on the information available for only two members out of a large number of taxa. Rather much variation can be expected in the embryological features matching well with the extensive diversification in vegetative and reproductive organs of taxa included in this family.

Chromosome counts of only two members, *Laurelia novaezelandiae* and *Kibara* sp. (Borgmann, 1964) have been made. Both genera show $n = 22$ but no karyotypic studies are available.

Calycanthaceae. The Calycanthaceae comprise two genera and about nine species distributed in the southeastern United States, Australia, China, and Japan.

The embryological literature has been summarized by Schnarf (1931). Recently Mathur (1969) has studied the development of male and female gametophytes in *Calycanthus*. The anther wall comprises the epidermis, fibrous endothecium, and glandular or periplasmodial tapetum. Meiosis in the microspore mother cell is abnormal. Cytokinesis is simultaneous resulting in tetrahedral or isobilateral tetrads. The mature pollen grains are 2-celled, rarely in tetrads in *Chimonanthus fragrans*, sterile and 2-nucleate. The exine is reticulate.

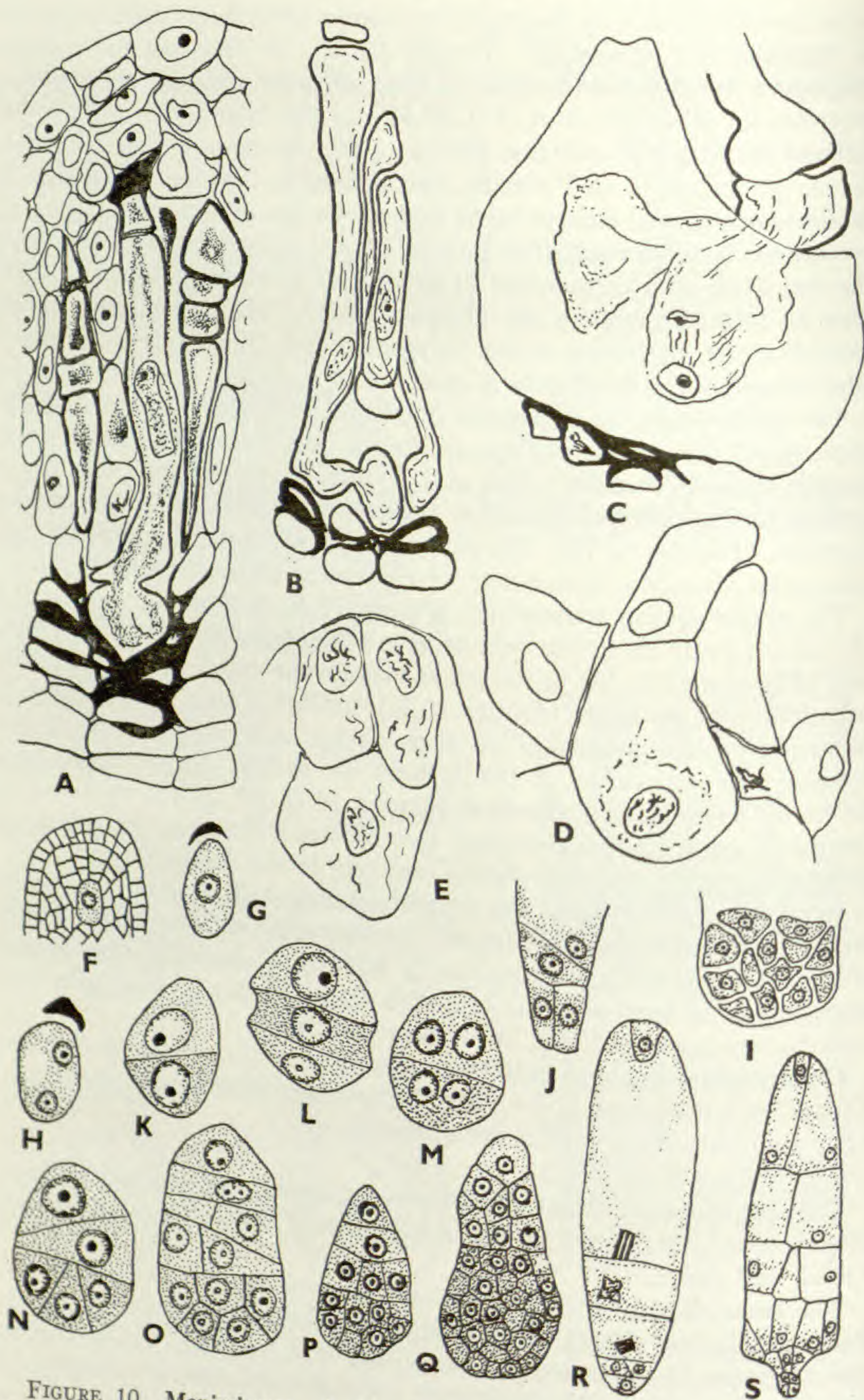


FIGURE 10. Monimiaceae. A, Nucellus with three megaspore tetrads; chalazal megaspore of central tetrad has grown out into an embryo-sac tube, ending in a chalazal vesicle immediately above the hypostase. B, Tubes from several tetrads, one from a micropylar megaspore — note nuclei still in tubes. C, Embryo sac plasma in nucellar cavity, still attached to mouth of embryo

The ovules are anatropous, bitegmic, and crassinucellate; the micropyle is formed by the inner integument alone. The cells of the nucellar epidermis divide periclinally to form a massive nucellar cap. The female archesporium is multicelled but parietal tissue is absent. Numerous megaspore mother cells function to form the linear tetrads, of which the chalazal megaspore functions to give rise to the Polygonum type of female gametophyte. Multiple embryo sacs are common. In the mature embryo sac the egg apparatus, one polar nucleus and the antipodal nuclei degenerate; syngamy and triple fusion therefore do not occur.

The development of the endosperm is autonomous and is *ab initio* cellular. Only nucellar embryos develop and polyembryony is frequent in *Calycanthus occidentalis*.

The two genera, *Calycanthus* and *Chimonanthus*, possess $n = 11$. The karyotype has not been investigated.

Lauraceae. The Lauraceae comprise about 31 genera and 2,250 species which are distributed in the tropics and warm-temperate areas of both hemispheres, especially Central and South America and southern Asia.

Of these, the embryology has been investigated only in *Cassytha* (Sastri, 1956, 1962), *Cinnamomum* (Chowdhury & Mitra, 1953; Giuliani, 1925; Sastri, 1958), *Laurus* (Battaglia, 1947; Mezzetti-Bambacioni, 1935, 1938, 1941), *Litsea* (Sastri, 1958), *Persea* (Schroeder, 1942, 1952), *Sassafras* (Coy, 1928), and *Umbellularia* (Mezzetti-Bambacioni, 1941).

The archesporium is multicelled and the wall layers are formed by the primary parietal layer (FIGURE 11 A). The anther wall comprises the persistent epidermis, fibrous or thick-walled endothecium, 2 middle layers, and amoeboid (*Cinnamomum*, *Laurus*, *Litsea*, *Persea*, *Sassafras*, *Umbellularia*) or glandular (*Cassytha*) tapetum (FIGURES 11 B-D). The tapetum is of parietal origin and its cells are bi-, tetra-, or multinucleate (FIGURES 11 B, C). Successive cytokinesis results in tetrahedral, isobilateral, T-shaped, or linear tetrads (FIGURES 11 E-G). The pollen grains are 2-celled, monocolpate or acolpate (*Cassytha*, *Laurus*). The exine is minutely spinescent.

The ovules are anatropous, bitegmic and crassinucellate. The micropyle is formed by both the integuments (FIGURE 12 B); in *Cassytha* (Sastri, 1962), however, the integuments do not grow beyond the nucellus so that the micropyle is broad and the overarching funiculus is in direct contact with the nucellus (FIGURE 11 K). The female archesporium is 1-celled (*Laurus*, *Umbellularia*) or multicelled as in *Cassytha* and *Cinnamomum* (FIGURES 11 H, J; 12 A). A massive parietal tissue is formed either from the parietal cell alone or by it and the nucellar epidermis

sac tube. D, Sporophytic buds in micropylar part of nucellar cavity, the bud is just appearing. E, Bud at 3-celled stage. F, Longitudinal section of nucellus with megaspore mother cell. G, H, One- and two-nucleate embryo sac, upper dyad cell degenerating. K-Q, Stages in embryogenesis. R, S, Stages in development of endosperm. (A-E, *Siparuna eggersii*, after Heilborn, 1931; F-S, *Peumus boldus*, after Mauritzon, 1935.)

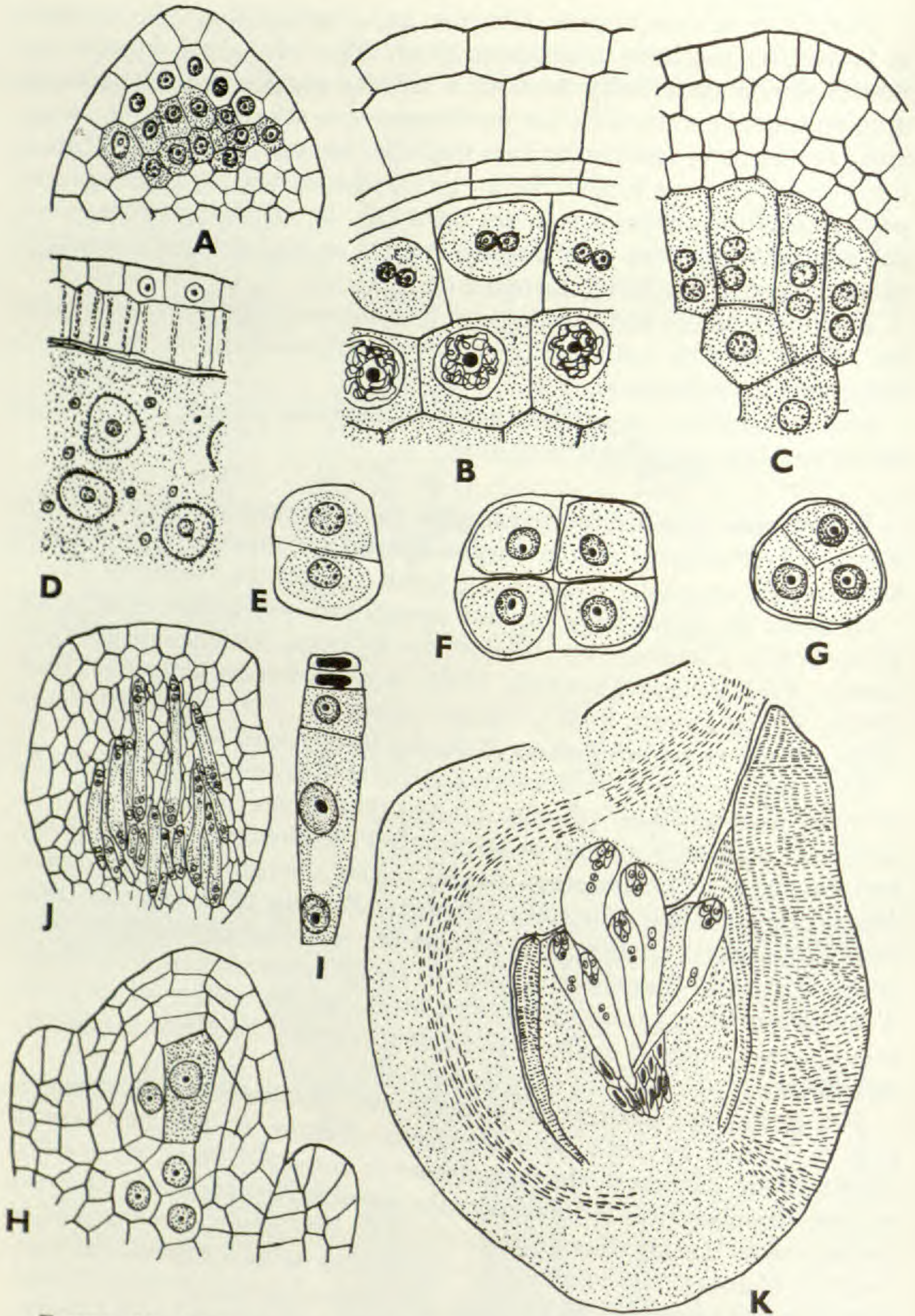


FIGURE 11. Lauraceae. A, Longisection of young ovule showing parietal layer and sporogenous cells. B, C, Transsection of part of anther lobe showing parietal wall layers and tapetum. D, Longitudinal section of portion of anther lobe showing fibrous endothecium, periplasmodial tapetum, and uninucleate pollen grains. E-G, Stages in the successive type of cytokinesis and formation of tetrads. H, Longitudinal section of ovule showing megaspore mother cell. I, Linear tetrad, the micropylar two degenerated, the chalazal one at 2-nucleate stage. J, Longitudinal section of nucellus showing elongation of numerous em-

(FIGURES 11 H, J; 12 A, B). Numerous megaspore mother cells function (FIGURES 11 J; 12 A) in *Cassytha* (Sastri, 1962), and *Litsea* (Sastri, 1958). The chalazal megaspore of the linear tetrad functions (FIGURE 11 I) and gives rise to the Polygonum type of female gametophyte. Multiple embryo sacs are formed in *Cassytha* (FIGURES 11 J, K), although occasionally twin embryo sacs have been observed in *Persea americana* (Schroeder, 1952) also. In *Cassytha filiformis* tips of 4 to 6 embryo sacs elongate, bore through the nucellus, and finally lodge themselves in the funiculus or inner integument (FIGURE 11 K). The synergids degenerate soon after fertilization but in *Litsea iners* they persist for some time. The antipodal cells (*Cinnamomum*, *Sassafras*, *Umbellularia*) or nuclei (*Cassytha filiformis*) are ephemeral (FIGURE 11 K) but in *Laurus nobilis* they persist, divide, and form an antipodal complex (Mezzetti-Bambacioni, 1935).

In *Cassytha filiformis* the development of the endosperm is *ab initio* cellular (FIGURES 12 D, E), whereas in all other members it is nuclear (FIGURE 12 C). The cell formation in the nuclear endosperm takes place at 4-celled or globular stages of the embryo. In *Cassytha* the first and the next transverse division in the chalazal chamber results in 3-celled endosperm (FIGURE 12 D). The middle cell then undergoes a vertical division. Divisions in all planes result in a massive tissue (FIGURE 12 E) which comes out of the nucellus at its tip and plugs the micropyle. Haustorial structures commonly found in the parasitic angiosperms are not met with in *Cassytha*.

The development of the embryo conforms to the Piperad (*Sassafras*), Asterad (*Persea americana*), or Onagrad (*Cinnamomum iners* and *Litsea sebifera*) types. Orientation of walls at the four-celled stage is variable (FIGURES 12 F-I). The mature embryo has a well-developed radicle and a shoot apex which develops two small leaf primordia oriented at right angles to the two cotyledons (FIGURE 12 J).

In *Cinnamomum*, *Litsea*, and *Cassytha* the seed coat is formed by the outer integument alone and comprises an epidermis of radially elongated cells, a few parenchymatous layers, and an inner epidermis of elongated cells having helical thickenings (FIGURE 12 L). The pericarp comprises an epidermis of tannin-filled cells, a fleshy zone of 7 to 9 layers of parenchymatous cells, a single layer of radially elongated cells, and an inner epidermis of lignified and pitted columnar cells. In *Cinnamomum* and *Litsea* an additional 4- or 5-layered zone of stone cells is also present beneath the outer tanniniferous epidermis.

Nearly seven genera out of 31 included in the family have been worked out cytologically (Chung *et al.*, 1963; Darlington & Wylie, 1955; Hair & Beuzenberg, 1960; Mangenot & Mangenot, 1957, 1958; Sharma & Bhatt, 1959; Suzuka, 1953). The genera *Beilschmiedia* (3 spp.), *Cinnamomum*

bryo sacs. K, Longitudinal section of ovule showing mature embryo sacs, two abutting the lysigenous cavity. (A, B, E-G, I-K, *Cassytha filiformis*; C, *Cinnamomum iners*; D, E, *C. zeylanicum*, after Sastri, 1958, 1962.)

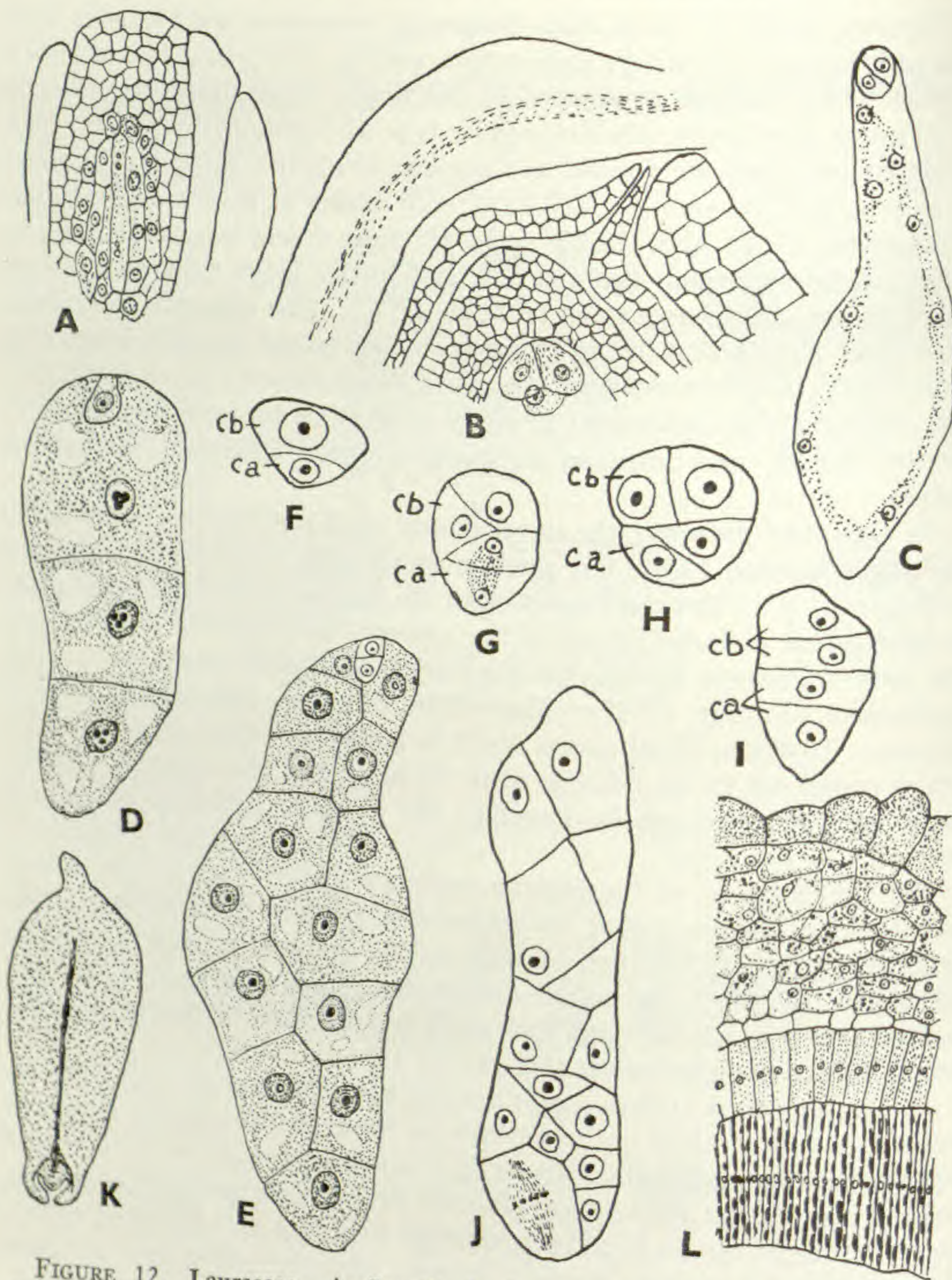


FIGURE 12. Lauraceae. A, Longitudinal section of ovule at four-nucleate embryo sac stage showing nucellar cells with prominent nuclei. B, Longitudinal section of apical region of ovule showing micropyle and egg apparatus. C, Longitudinal section of embryo sac showing endosperm nuclei and two-celled proembryo. D, E, Development of cellular endosperm. F-J, Stages in embryo-first two leaves. K, Mature embryo in paracotyledonary view showing primordia of first two leaves. L, Longitudinal section of part of seed coat. (A-C, *Cinnamomum iners*; D-L, *Cassytha*, after Sastri, 1958, 1962.)

(9 spp.), *Lindera* (4 spp.), *Persea* (4 spp.), *Sassafras* (1 sp.), and *Umbellularia* (1 sp.) all possess $n = 12$. Only *Laurus* shows $2n = 36$ in *L. canariensis* and $2n = 42, 48$ in *L. nobilis*. The basic number of the family perhaps may be $x = 12$.

Trochodendraceae. Trochodendraceae is a monotypic family comprising *Trochodendron aralioides* distributed in Japan and Formosa.

Bailey and Nast (1945), and Nast and Bailey (1945) have studied the vegetative anatomy and floral morphology of *T. aralioides*, whereas Yoffe (1962, 1965) has investigated its embryology.

At the microspore-mother-cell stage the anther wall consists of an epidermis, the endothecium, two or three middle layers, and a two-layered glandular tapetum having binucleate cells (FIGURE 13 A). During maturation the epidermal cells of the anther wall become protuberant and develop cuticular fibrillar projections along their outer surface (FIGURE 13 B). The endothecium becomes very prominent by developing broad bands of fibrous thickenings; the middle layers become flattened and crushed. The tapetum, however, persists during the complete meiotic process in the microspore mother cells until the formation of two-celled pollen grains (FIGURE 13 B). At this stage the tapetal layer adjacent to the middle layers degenerates, whereas the one next to it develops Ubisch granules along the lateral and inner walls of the tapetal cells (FIGURE 13 B). Meiosis is normal but occasionally, a cell plate is formed during telophase I which, however, disappears later. The cytokinesis is of the simultaneous type and the resulting tetrads are tetrahedral. The nucleus of the microspore moves towards one side where it divides to form the generative and the vegetative cells. The mature pollen grains are 2-celled and tricolpate having a reticulate exine.

The ovules are anatropous, bitegmic, and crassinucellate (FIGURE 13 C). The inner integument is initiated first, followed by the outer, but the micropyle is formed by the inner integument alone (FIGURE 13 C). At the mature embryo-sac stage, the chalazal end of the ovule is transformed into a well-developed long, tapering projection. The vascular supply of the ovule enters this projection and curves backwards to end at the base of the chalazal region (FIGURE 13 C).

A single hypodermal archesporial cell cuts off a parietal cell which divides repeatedly to form a 3- or 4-layered parietal tissue. After meiosis I a dyad is formed which subsequently develops into either a T-shaped or linear tetrad. The chalazal megaspore functions (FIGURE 13 D) to give rise to a 2-nucleate, 4-nucleate (FIGURE 13 E) and 8-nucleate embryo sac of the Polygonum type (FIGURE 13 F). The synergids possess a conspicuous filiform apparatus; the antipodal cells are uninucleate and persistent (FIGURE 13 F).

Syngamy and triple fusion occur simultaneously. The development of the endosperm is *ab initio* cellular. The first division is transverse giving rise to a large micropylar and very small chalazal chamber (FIGURE 13 G). The next division in the micropylar chamber is transverse, while in the chalazal chamber it is vertical (FIGURE 13 H). Repeated divisions in both the chambers result in a massive endosperm tissue. However, the cells formed in the chalazal chamber are small and densely cytoplasmic. The major part of the endosperm tissue is formed by the micropylar chamber (FIGURE 13 I).

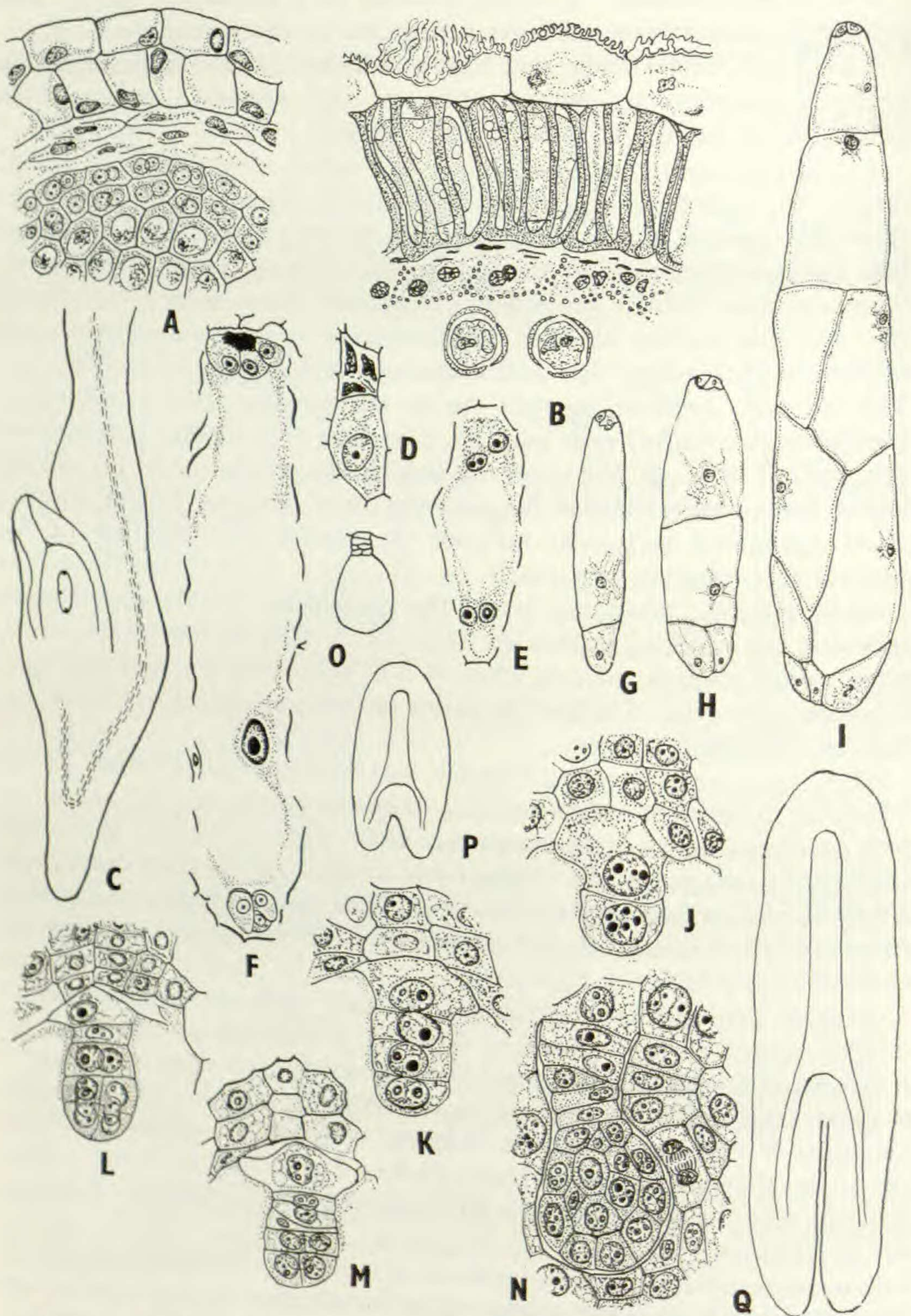


FIGURE 13. Trochodendraceae. A, Transection of part of anther lobe at microspore-mother-cell stage. B, Same, at time of dehiscence of anther — note cuticular protuberances in epidermis. C, Longisection of ovule at mature embryo sac stage, note circumscutous vascular supply. D, Tetrad of megaspores, upper three degenerated and chalazal megaspore functional. E, Four-nucleate embryo sac. F, Mature embryo sac. G-I, Stages in development of endosperm. J-Q, Stages in development of a dicot embryo. (A-Q, after Yoffe, 1962, 1965.)

The zygote divides transversely forming the two cells, *ca* and *cb* (FIGURE 13 J). Subsequent division in both these cells is transverse thus resulting in a 4-celled linear proembryo (FIGURE 13 K). The terminal cell of this proembryo divides vertically followed by another similar division at right angles to the first. The four cells thus formed divide transversely to form the octant disposed in 2 tiers of 4 cells each (FIGURE 13 L). Repeated divisions in this octant give rise to a globular proembryo (FIGURE 13 N, O). By this time the other 3 cells divide transversely and longitudinally and produce a suspensor (FIGURE 13 N). The globular proembryo differentiates first into a heart-shaped and later into a dicotyledonous embryo (FIGURE 13 P). At this stage the procambial strand is well developed (FIGURE 13 Q).

The seed coat is formed by both the integuments. In the mature seed the inner epidermis of the outer integument becomes thick-walled and sclerenchymatous to constitute the hard part of the seed coat whereas the other layers of the two integuments remain thin-walled. In the mature seeds the tapering chalazal projection becomes transformed into the wing.

The basic number of this monotypic family also is $n = 19$ in *Trochodendron aralioides* (Whitaker, 1933).

Cercidiphyllaceae. The genus *Cercidiphyllum*, which includes two species, *C. japonicum* and *C. magnificum*, constitutes the family Cercidiphyllaceae having a restricted distribution in Japan and China.

Swamy and Bailey (1949) have investigated the morphology, anatomy, and embryology of *Cercidiphyllum japonicum*. The structure and development of the anther resembles the majority of dicotyledons. The tapetum is, however, glandular with binucleate cells. The process of cytokinesis after reduction divisions is of the simultaneous type resulting in microspore tetrads. The pollen grains at the shedding stage are 2-celled, spherical, and tricolpate; the colpi are conspicuously broad. The exine is finely pitted.

The ovules are hemianatropous, bitegmic, and crassinucellate. The two integuments are initiated almost at the same time; the outer integument soon overgrows the inner, although in a mature ovule both the integuments take part in the formation of micropyle. The chalazal end of the ovule develops into a flattened tapering projection which forms a wing in the mature seed. After fertilization the vascular bundle reaches the middle of the tapering chalazal projection and then bends to end at the base of the nucellus.

The female archesporium is single-celled, forming five or six parietal cells (FIGURE 14 A). Periclinal divisions in the nucellar epidermis add to the formation of a massive parietal tissue, resulting in a deeply seated megaspore mother cell in the nucellus (FIGURE 14 A). The megaspore mother cell undergoes meiosis thus giving rise to a linear tetrad. The three micropylar megaspores degenerate while the chalazal one functions (FIGURE 14 A) to form an eight-nucleate embryo sac of the Polygonum type (FIGURE 14 B). The egg apparatus is conspicuous, three antipodal

cells are uninucleate while the two polar nuclei fuse before fertilization (FIGURE 14 B).

The primary endosperm nucleus moves to the chalazal part of the embryo sac where it divides, followed by formation of a transverse wall resulting in a large micropylar and a small chalazal chamber (FIGURE 14 C). Subsequent divisions in the two chambers are essentially transverse until a 10- to 12-celled uniseriate endosperm is formed (FIGURE 12 D). During this growth period the embryo sac enlarges considerably and comes to be in close contact with the vascular strand (FIGURE 14 F). Further divisions occur in all planes finally producing a compact mass of endosperm tissue (FIGURE 14 E), most of which, however, is consumed by the developing embryo.

The zygote divides transversely to form the cells *ca* and *cb*. The basal cell *cb* enlarges conspicuously without undergoing any further divisions (FIGURE 14 G); whereas the terminal cell *ca* divides again transversely (FIGURE 14 H). Subsequent divisions in the derivatives of the terminal cell are vertical to organize the quadrant and octant (FIGURES 14 I, J). The cells of the octant divide further and form a globular proembryo (FIGURES 14 K, L). In the mature seed the embryo possesses a long hypocotyl and two cotyledons which enclose the embryonal shoot apex. The embryogeny, therefore, is of the Solanad type.

The seed coat is formed by the outer integument alone. In the region of the wing it becomes flattened so that the chalazal wing appears to extend beyond it at either side.

Of the two species of *Cercidiphyllum* included, chromosome counts have been made for *C. japonicum*, which is $n = 19$ (Whitaker, 1933). No karyotypic analysis is available.

MORPHOLOGY AND ANATOMY

A comparative study of the morphology and anatomy of the ranalian families has yielded many fundamental concepts and their further phylogenetic amplification. The work is exhaustive and voluminous and will not be repeated here for want of space. For detailed information the reader is referred to the chief publications on Magnoliaceae (Canright, 1952, 1953, 1955, 1960, 1963, 1965; Lemesle, 1933, 1953; McLaughlin, 1933; Ozenda, 1913; Tucker, 1959, 1961), Winteraceae (Bailey, 1944a, b; Bailey & Nast, 1943a,b, 1944a,b, 1945; Tucker, 1960), Degeneriaceae (Swamy, 1949), Himantandraceae (Bailey, Nast & Smith, 1943), Wettstein, 1935; Wilson, 1960, 1964, 1965; Vestal, 1935), Annonaceae (Wyk & Canright, 1956; Ozenda, 1947), Eupomatiaceae (Lemesle, 1938), Myricaceae (Garrat, 1933a,b; Nair & Bahl, 1956), Canellaceae, Schisandraceae (Bailey & Nast, 1948; Jalan, 1968; Smith, 1947), Illiciaceae (Bailey & Nast, 1948; Lemesle, 1945; Smith, 1947), Austrobaileyaceae (Bailey & Swamy, 1949), Trimeniaceae, Amborellaceae, and Monimiaceae (Bailey & Swamy, 1948; Money, Bailey, & Swamy, 1950), Calycanthaceae (Fahn & Bailey, 1957; Smith, 1928), Gomortegaceae (Money, Bailey, & Swamy,

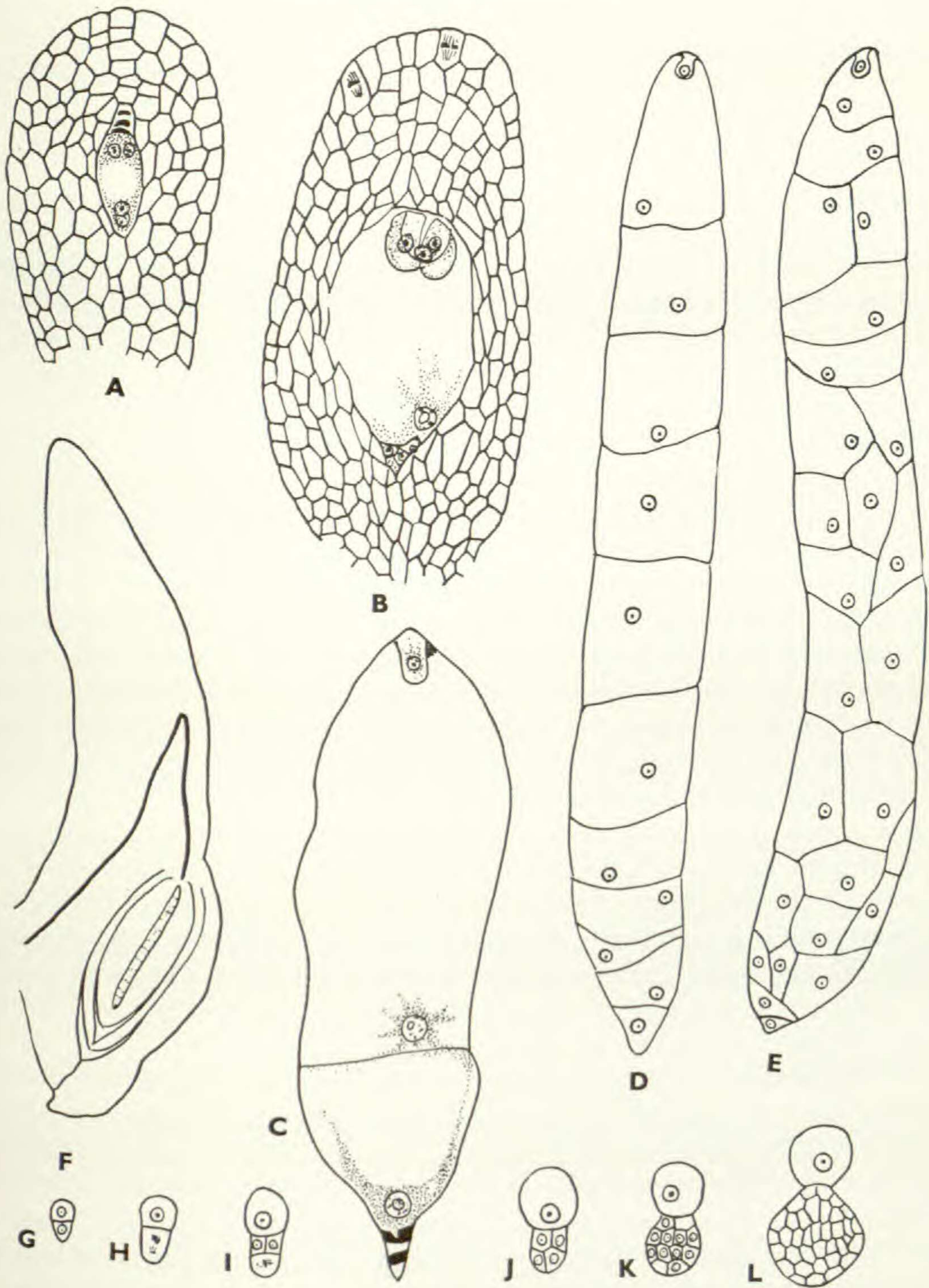


FIGURE 14. *Cercidiphyllaceae*. A, Longitudinal section of nucellus showing four-nucleate embryo sac. B, Same, showing mature embryo sac. C-E, Stages in development of endosperm. F, Longitudinal section of ovule showing early stages in formation of endosperm. G-L, Stages in development of the embryo —note that basal cell does not divide and contribute much in formation of embryo proper. (A-L, after Swamy & Bailey, 1949.)

1950), Lauraceae (Coy, 1928; Sastri, 1952; Stern, 1954), Hernandiaceae (Shutts, 1960), Tetracentraceae and Trochodendraceae (Bailey & Nast, 1945; Croizat, 1947; Nast & Bailey, 1945; Smith, 1947), and *Cercidiphyllaceae* (Swamy & Bailey, 1949). Eames (1961) has given an excellent

review on Ranales which outlines in brief, the principal trends of specializations in the group.

INTERRELATIONSHIPS

General considerations. **ANTHER WALL.** In almost all the families the basic architecture of the structure of the anther wall is uniform and comprises the epidermis, fibrous endothecium, 2 to 4 middle layers, and tapetum. The epidermis is persistent till the dehiscence of the anther; Trochodendraceae stands apart from the rest of the families in having prominent fibrillar cuticular thickenings on the outer surface. The fibrous endothecium (excepting *Magnolia stellata*; Kapil & Bhandari, 1964) is persistent and mostly 1-layered. However, in Magnoliaceae (Hayashi, 1960; Kapil & Bhandari, 1964; Padmanabhan, 1960), Degeneriaceae (Swamy, 1949), Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968; Swamy, 1949), and Schisandraceae (Kapil & Jalan, 1964), there is a tendency for it to become irregularly 2-layered along the outer face of the anther wall while some layers of the connective tissue toward the inner side also develop fibrous thickenings and simulate the endothecium. Its maximum amplification is found in the relatively more primitive families Winteraceae and Degeneriaceae, and perhaps indicates that it is a primitive feature and that the phylogenetic trend proceeds toward the reduction of the endothelial tissue.

The middle layers vary from 2 to 4 in number and again in Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Illiciaceae, and Canellaceae 1 or 2 middle layers persist even at the time of dehiscence of the anther, whereas there is a decrease in the number of the middle layers in Myristicaceae, Monimiaceae, Lauraceae, and Trochodendraceae. They are ephemeral and become completely crushed during and after meiosis in Myristicaceae, Lauraceae, and Trochodendraceae.

ANTHER TAPETUM. The families Austrobaileyaceae, Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Myristicaceae, Canellaceae, Schisandraceae, Illiciaceae, Monimiaceae, Calycanthaceae, Trochodendraceae, and Cercidiphyllaceae resemble each other in having glandular tapetum. In *Annona* (Juliano, 1935; Asana & Adatia, 1947) and *Polyalthia*, *Unona*, and *Cananga* (see Asana & Adatia, 1947) of the Annonaceae, most Lauraceae excepting *Cassytha* (Sastri, 1962), and *Pseudowintera colorata* (Bhandari, 1963c) of the Winteraceae, amoeboid tapetum has been reported. The occurrence of amoeboid tapetum in the Annonaceae is questioned by Periasamy and Swamy (1959) first because of lack of proper illustrations in the works of Juliano (1935) and Asana and Adatia (1947), and because they found glandular tapetum in *Cananga odorata* whereas Asana and Adatia (1947) had earlier reported amoeboid tapetum in this species. It may turn out that Annonaceae have only glandular tapetum. Of the three genera of the Winteraceae investigated, *Drimys*, *Pseudowintera*, and *Zygogynum*, only one species, *Pseudowintera colorata* (Bhandari, 1963c) possesses amoeboid tapetum. The other species *P. axillaris*

(Sampson, 1963) has glandular tapetum. Furthermore, an earlier report of amoeboid tapetum in *Drimys* (Kutti Amma, 1938) has been refuted recently by Bhandari and Venkataraman (1968). Therefore, Lauraceae is the only family where amoeboid tapetum can be regarded as a family character.

Glandular tapetum, therefore, reflects a primitive pattern whereas the amoeboid tapetum is a phylogenetic departure. In the Ranunculales, the herbaceous Ranales, a parallel trend can also be observed, although the amoeboid tapetum occurs more frequently in this group.

In Magnoliaceae and Trochodendraceae the glandular tapetum is bilayered while in Schisandraceae and Illiciaceae it becomes irregularly bilayered. In the rest of the families it is uniformly 1-layered. The presence of Ubisch granules binds the Magnoliaceae, Trochodendraceae, and Canellaceae together. In the last family, however, the granules are studied along the inner as well as outer faces of the tapetal walls. The cells of the tapetum are uninucleate in Myristicaceae, binucleate in Magnoliaceae, Degeneriaceae, Annonaceae, Illiciaceae, Trochodendraceae, and Cercidiphyllaceae, and multinucleate in Magnoliaceae, Annonaceae, Canellaceae, Schisandraceae, Monimiaceae, and Lauraceae with a tendency to form polyploid nuclei by fusion.

ORIGIN OF TAPETUM. The sporogenous origin of the tapetum has been looked at suspiciously and this was particularly true in some instances since a reinvestigation proved its parietal origin at least along the outer (protuberant) face of the anther locule (*see* Maheshwari, 1950). Recently, Swamy and Periasamy (1966) argued that the tapetum is of dual origin, contributed by parietal tissue along the outer side, and by the connective or septal tissue along the inner side of the locule (*see also* Coulter & Chamberlain, 1905). This conclusion has been further supported by ontogenetic studies of anther wall development in *Anemone rivularis* (Bhandari, 1968). Bhandari (1968) has suggested a reappraisal of the sporogenous origin of tapetum and it may be in some instances that this tissue does change its function from reproductive to nutritional as is the case in most of the gymnosperms. Such a situation has been observed in Annonaceae. In *Annona* (Juliano, 1935), *Cananga odorata*, and *Miliusa wightiana* (Periasamy & Swamy, 1961) the microspore mother cells are separated by septae which originate from the sporogenous tissue and behave like the tapetum developing from the parietal tissue. In such members of Annonaceae, therefore, the tapetum is contributed partly by the sporogenous tissue and partly by the parietal tissue. Hayashi (1960) has reported sporogenous origin of the tapetum in *Magnolia liliflora* and *M. virginiana*. The Magnoliaceae and Annonaceae thus share this feature.

CYTOKINESIS AND MICROSPORE TETRADS. Cytokinesis in microspore mother cells at the end of the first or second meiotic division is another important character. It is simultaneous in Austrobaileyaceae, Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae (some members), Canellaceae, Schisandraceae, Illiciaceae, Monimiaceae, Calycanthaceae Trochodendraceae, and Cercidiphyllaceae, whereas in Annonaceae (some members),

Myristicaceae, and Lauraceae it is of the successive type. Sastri (1957) is of the opinion that in Annonaceae a series exists from the successive type of cytokinesis in *Annona reticulata*, *Asimina triloba*, and *Uvaria kirkii* to the simultaneous type in *Saccopetalum tomentosum* and *Polyalthia*, through intermediate types like *Annona cherimolia* and *A. squamosa* where the first constriction, although initiated at the end of heterotypic division, is delayed, and completed only along with the other after the homotypic division. A similar situation is also met with in *Magnolia* (Kapil & Bhandari, 1964, *see also* Farr, 1918), *Zygogynum baillonii* (Swamy, 1952) of the Winteraceae, and *Trochodendron* (Yoffe, 1962). Periasamy and Swamy (1959) on the other hand, consider the successive type of cytokinesis of the Annonaceae to be of modified simultaneous type. The present author is not in agreement with Periasamy and Swamy (1959) and considers that if a dyad is formed at the end of the heterotypic division as in *Asimina* and *Uvaria*, it should be regarded as the successive type irrespective of its formation, by cell plate or by furrowing. The preponderance of the simultaneous type of cytokinesis in the majority of the Magnolian taxa and the occurrence of the intermediate forms where the first furrow is initiated after heterotypic division, together with the formation of an evanescent cell plate in primitive genera like *Zygogynum baillonii* (Swamy, 1952), *Pseudowintera axillaris* (Sampson, 1963), *Drimys winteri* (Bhandari & Venkataraman, 1968), and *Magnolia* (Kapil & Bhandari, 1964) might indicate that the successive type is a derived condition (*see also* Maheshwari, 1950).

At the end of meiosis tetrahedral tetrads are formed in Canellaceae, Illiaceae, Monimiaceae, and Trochodendraceae, and tetrahedral or decussate tetrads in the Magnoliaceae, Winteraceae, Schisandraceae, Calycanthaceae, and Cercidiphyllaceae. Tetragonal tetrads are found in Degeneriaceae and Annonaceae, while in Myristicaceae only the isobilateral type occurs. In the Lauraceae, tetrahedral, isobilateral, linear, or T-shaped types of tetrads are met. Two trends are evident: (1) the retention of the microspores within the microspore mother cell until they are partially mature and their delayed release as in Degeneriaceae (Swamy, 1949) and Canellaceae (Parameswaran, 1962); and (2) the shedding of the pollen grains in permanent tetrads as in Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968), Lactoridaceae, and occasionally also in Annonaceae (*see* Parulekar, 1967), and Magnoliaceae (Canright, 1953).

GENERATIVE CELL. In all the families the pollen grains are shed at the two-celled stage. The mode of cutting off of the generative cell is very specific but at the same time very difficult to ascertain since the division of the microspore nucleus takes place after they are released from the tetrads. In the Austrobaileyaceae, Degeneriaceae, Annonaceae, and in abnormal tetrads of *Magnolia* (Canright, 1962), the generative cell is cut off towards the distal pole, while in Winteraceae and Canellaceae it is formed towards the proximal end. In Degeneriaceae and Canellaceae, however, the microspores become two-celled within the tetrads.

OVULE. The ovules are anatropous, bitegmic, and crassinucellate in

Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Myristicaceae, Schisandraceae, Illiciaceae, Monimiaceae, Calycanthaceae, Lauraceae, Trochodendraceae, and Cercidiphyllaceae. In some members of Annonaceae, however, the ovules are tritegmatic and in Canellaceae they may also be hemianatropous. In *Siparuna* of the Monimiaceae the ovules are unitegmatic. In the Magnoliaceae, Degeneriaceae, and Annonaceae the outer integument is vascularized whereas in others, the funicular supply ends at the base of the nucellus. The micropyle is formed by both the integuments in Magnoliaceae, Annonaceae, Canellaceae, Schisandraceae, Illiciaceae, Lauraceae, and Cercidiphyllaceae while in Degeneriaceae, Winteraceae, Myristicaceae, Monimiaceae, Calycanthaceae, and Trochodendraceae it is formed by the inner integument. The micropyle is zigzag in Canellaceae, whereas it is straight in the other families. The family Trochodendraceae (Yoffe, 1965) and Cercidiphyllaceae (Swamy & Bailey, 1949) resemble each other in having a chalazal tapering projection; the funicular vascular supply enters the projection for some distance and then bends back to end at the base of the nucellus. This projection forms a wing-like structure in the seed.

The massive parietal tissue is formed by the parietal cell alone in Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Schisandraceae, Illiciaceae, and Trochodendraceae. In Monimiaceae and Cercidiphyllaceae it develops from both the primary parietal cell and the nucellar epidermis, while in Calycanthaceae it originates from nucellar epidermis alone. The family Lauraceae, however, exhibits both the trends where the parietal tissue is formed by the parietal cell alone or together with the nucellar epidermis. Although the relic feature of producing a massive parietal tissue is retained, the evident phylogenetic trend is towards the suppression of the formation of this tissue from the primary parietal cell, a trend which becomes well established in some of the herbaceous ranalian families such as Ranunculaceae (some members), Berberidaceae, Lardizabalaceae, and some members of Menispermaceae (*see* Bhandari, 1962, 1963b, 1965, 1968; Bhatnagar, 1965; Johri, 1936; Joshi, 1939; Sastri, 1964; Swamy, 1953). A prominent nucellar cap is met with in Monimiaceae, Calycanthaceae, and Lauraceae (Heilborn, 1931; Mauritzon, 1935; Sastri, 1963; Schnarf, 1931). A conspicuous hypostase is met with in Magnoliaceae (Kapil & Bhandari, 1964), Degeneriaceae (Swamy, 1949), Annonaceae (Corner, 1949), and Monimiaceae (Mauritzon, 1935).

MEGASPOROGENESIS AND FEMALE GAMETOPHYTE. The female archesporium is hypodermal, 1-celled in the families Degeneriaceae (Swamy, 1949), Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968; Sampson, 1963; Swamy, 1952), Myristicaceae (Schnarf, 1931), Canellaceae (Parameswaran, 1962), Illiciaceae (Yoshida, 1962), Trochodendraceae (Yoffe, 1965), and Cercidiphyllaceae (Swamy & Bailey, 1949) but multicelled in Schisandraceae (Kapil & Jalan, 1964; Yoshida, 1962), Calycanthaceae (Schnarf, 1931), and Lauraceae (Sastri, 1963). In the Magnoliaceae (Kapil & Bhandari, 1964; Padmanabhan, 1960), Annonaceae (Parulekar, 1967), and Monimiaceae (Heilborn, 1931; Mauritzon, 1935) the archesporium may be 1- to multicelled. The tendency, however,

is towards the reduction in the number of archesporial cells as is evident in Magnoliaceae (Kapil & Bhandari, 1964) where, although numerous archesporial cells differentiate, ultimately only one functions. Only in the Lauraceae and Calycanthaceae do large numbers of megaspore mother cells function simultaneously, these have perhaps retained the ancestral feature of forming functional massive sporogenous tissue. In *Siparuna* of the Monimiaceae (Heilborn, 1931) the ovules are unitegmic but have a multicelled archesporium, a combination of advanced and primitive features.

In almost all the families the development of the female gametophyte conforms to the *Polygonum* type. In *Schisandra grandiflora* (Kapil & Jalan, 1964) and *Schisandra chinensis* (Yoshida, 1962), the *Polygonum* type of female gametophytes has been reported, whereas Swamy (1964) observed the *Oenothera* type, and a unique bisporic type (organizing after 4-nucleate stage) in *S. chinensis*. The *Allium* type of embryo sac has also been recorded in *Peumus boldus* (Mauritzon, 1936) of the Monimiaceae. It is evident, therefore, that although wall formation takes place after meiosis I and II, resulting in a tetrad of megaspores in a majority of the Magnolian members, there is a tendency towards suppression of the cytokinesis after homotypic division, hence towards a bisporic type.

The synergids and the antipodal cells or nuclei (*Cassytha*, Sastri, 1962) are characteristically ephemeral excepting in *Peumus* where secondary multiplication occurs to form the antipodal cell complex. The polar nuclei fuse before fertilization, which is porogamous. Multiple embryo sacs are reported in Lauraceae (Sastri, 1962), occasionally twin embryo sacs are met with in *Magnolia* (Kapil & Bhandari, 1964) and *Drimys winteri* (Bhandari & Venkataraman, 1968). Embryo sac haustoria are found only in *Cassytha* (Sastri, 1962).

ENDOSPERM. The endosperm is *ab initio* cellular in the Magnoliaceae (Kapil & Bhandari, 1964; Padmanabhan, 1960), Degeneriaceae (Swamy, 1949), Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968), Annonaceae (Periasamy & Swamy, 1958), Schisandraceae (Kapil & Jalan, 1964), Illiciaceae (Hayashi, 1963), Monimiaceae (Mauritzon, 1935), Calycanthaceae (Schnarf, 1931), *Cassytha* (Sastri, 1962), Trochodendraaceae (Yoffe, 1965), and Cercidiphyllaceae (Swamy & Bailey, 1949). The endosperm is nuclear only in Myristicaceae and Lauraceae (excepting *Cassytha*). In Calycanthaceae its development is reported to be autonomous. The division of the primary endosperm nucleus is transverse (rarely vertical in *Pseudowintera colorata*, see Bhandari, 1963c) and even further segmentation is very characteristic and similar in a large number of Magnolian members, thus producing a uniseriate file of cells. Later, divisions in all planes result in a massive endosperm tissue. *Magnolia obovata* (Kapil & Bhandari, 1964) is the only record of the presence of a 2- or 3-celled chalazal endosperm haustorium. The families Degeneriaceae (Swamy, 1949), Annonaceae (Corner, 1949; Periasamy & Swamy, 1961), Myristicaceae (Periasamy, 1961), and Canellaceae (Parameswaran, 1961) resemble each other in having ruminant endosperm. However, the tissue causing rumination is histologically different in various families. In De-

generiaceae (Swamy, 1949) and Annonaceae (Periasamy, 1962; Periasamy & Swamy, 1961) the ruminating projections develop from the outer integument, while in Myristicaceae (Periasamy, 1961) they originate from the meristematic chalaza. For Canellaceae (Parameswaran, 1961), however, such details are not known.

The presence of cellular endosperm in most members of the Magnoliales and allies seems to indicate the primitiveness of this feature, and the restricted occurrence of the nuclear type may be a phylogenetic advancement. This is also confirmed by the fact that in the Ranunculales most herbaceous members have nuclear type. The presence of a haustorium which is not very aggressive is inexplicable; whether this is the preservation of a relic feature or a phylogenetic advancement which was to be well established in many other groups of angiosperms remains highly speculative. The latter possibility appears to be more sound.

EMBRYOGENY. In some members of Magnoliaceae (Kapil & Bhandari, 1964), Degeneriaceae (Swamy, 1949) and Winteraceae (Bhandari & Venkataraman, 1968) the early segmentation is rather irregular, although at the preglobular or globular stages the embryogenesis proceeds normally and forms a healthy embryo. In other families, wherever information is available, the pattern of development becomes established and is mostly of the Onagrad (Annonaceae), Onagrad or Asterad (Schisandraceae, Lauraceae), Asterad (Illiciaceae, Monimiaceae), or Solanad type (*see* Davis, 1966). However, one basic factor evident throughout is that the basal cell, *cb*, has little or no role in the organization of the embryo proper and forms the major part of the suspensor.

SEED COAT. In the Magnoliaceae, Winteraceae, Degeneriaceae, Annonaceae, Myristicaceae, Lauraceae, and Cercidiphyllaceae the seed coat is constituted chiefly by the outer integument while the inner integument degenerates and its remnants may persist. In Canellaceae, Schisandraceae, and Trochodendraceae, however, both the integuments take part in formation of the testa. In the Magnoliaceae and Degeneriaceae the seed coat is differentiated into outer fleshy and inner stony regions but in the rest of families the seed possesses a hard seed coat. In the Winteraceae it is mostly the enormously radially elongated outer epidermis which constitutes the seed coat while the rest of the layers become slightly thick walled. In Canellaceae and Trochodendraceae the outer epidermis of the outer integument and the inner epidermis of the inner integument become sclerenchymatous whereas the rest of the layers remain thin walled. The Schisandraceae possess an elaborate seed structure (*see* Kapil & Jalan, 1964), having outer integument comprising the epidermis of macrosclereids, 2 or 3 subepidermal layers of brachysclereids, and 2 or 3 parenchymatous layers. The inner integument also persists as a thin layer of degenerated thick-walled cells. In Degeneriaceae, Myristicaceae, Canellaceae, and Annonaceae the ruminations in the seed are produced by the outer integument. The Trochodendraceae and Cercidiphyllaceae possess a tapering chalazal projection which develops into a wing-like structure in the mature seed.

[*To be continued*]